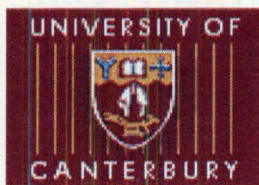

The growth of cultured *Perna canaliculus* in Pelorus Sound, New Zealand: the importance of spat origin, environment, and time of harvest

**A thesis submitted in partial fulfilment
of the requirements of the Degree of
Doctor of Philosophy in Zoology
at the University of Canterbury**

by

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ABSTRACT

Factors affecting the growth and condition (flesh weight/total weight) of the greenshell® mussel, *Perna canaliculus*, were investigated in Pelorus Sound, on the northern coast of the South Island of New Zealand. The relative importance of time of harvest, location (two mussel farms in each of three areas), and the geographic origin of mussels (three stocks: Golden Bay, Kaitaia, and the Marlborough Sounds) were measured in four growth trials between August 1997 and October 1999.

Particular attention was paid to the condition cycles of mussels because poor condition during winter often results in a severe reduction in yields and/or the cessation of commercial harvesting. If certain mussel stocks, or mussels grown in particular areas of Pelorus Sound, remain in better condition during winter, the selective harvesting of these mussels would potentially increase yields.

The condition of mussels declined sharply in mid-winter. This coincided with a rapid decline in the number of mussels with mature gonads and an increase in the number of mussels with immature gonads. This indicates spawning causes the poor condition of farmed mussels in winter. Following winter spawning in both 1998 and 1999 the condition index of mussels at all six study sites declined to very low levels (<c. 30%) regardless of pre-spawning condition. Outside the winter spawning period mussels with high condition indices (c. 40-50%) were nearly always available.

Stock had a significant, although small, effect on the condition cycle of mussels. Immediately following winter spawning the condition index of the stock originating from Golden Bay was c. 2-3% higher than the stock from Kaitaia. The period of time that the Golden Bay stock remained in better condition did, however, vary between one and four months in the four growth trials. Because the differences in condition cycles between stocks were small and the length of time that the Golden Bay stock was in better condition varied, it would be difficult to increase the yields from farmed mussels by selectively harvesting stocks at different times of the year. There was also no evidence that growing particular mussel stocks in specific areas of Pelorus Sound could enhance yields.

The shell growth rate of Golden Bay stock was c. 25% greater than Marlborough Sounds and Kaitaia stock in the first of the four growth trials. This did not occur in subsequent trials. The difference in growth in the first trial was

attributed to the stocks being grown at different locations in Pelorus Sound prior to the trial. If this is the case, it may be feasible to enhance the growth of farmed mussels by manipulating the environment (e.g. location) that spat are exposed to early in life. Because previous studies did not expose mussel stocks to the same environments prior to the experiments, or attempt to repeat trials, the stock-related traits they identified may not be predictable or consistent features of the stocks.

Spatial and temporal factors (the location and timing of sampling) were the key determinants of mussel condition. The largest range in condition index between sites at a single time was 23% (August 1998), and the largest range between times within a site (Hallam Cove) was 22%. This is in contrast to the largest difference in condition between stocks, of 7% (between Golden Bay and Kaitaia stocks in June 1999). The range in condition (and commercial yields) of mussels between study sites and times was therefore highly variable.

Between August 1998 and March 1999 mussels in the middle area of the Sound declined in condition from c. 50% to 30%. This change in condition was not related to any clear annual cycle and suggests the amount of mussels that the Sound (or parts thereof) can sustain may change through time. This is an important point for fisheries managers to consider, as a 300% increase in mussel production has been proposed for Pelorus Sounds region.

The rate at which mussels recovered from winter spawning varied between the inner, middle, and outer areas of Pelorus Sound and also between years. Following spawning in 1998, the condition of mussels in the middle area of Pelorus Sound recovered quickly and the commercial harvest rapidly returned to pre-spawning levels. Although the rate at which mussels recovered also varied between areas in 1999, condition recovered more slowly and harvests following winter spawning were lower than in 1998.

The conclusion of this study is that although stock has a statistically significant (but small) influence on the condition cycle of farmed *P. canaliculus*, location and time of harvest are the key determinants of condition and commercial yield. Mussel farmers are therefore advised to locate farms across a broad range of areas in Pelorus Sound. This will allow them to exploit the high degree of spatial variability in mussel condition, to minimise the impact of winter spawning events, and therefore maximise yields throughout the year.

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Chapter 1

General Introduction

1.1 INTRODUCTION

The global demand for fish and bivalves has grown rapidly over the last 25 years (Jonson 2000). This has increased the pressure on many wild fisheries. In 1999, the Food and Agriculture Organisation (FAO) reported that more than 75% of fish stocks were exploited at or above their maximum sustainable yield (FAO web site, 2001). Reductions in catch rates and quotas have led many fishing companies to diversify into aquaculture. This has resulted in a substantial increase in global aquaculture production: between 1987 and 1996 the volume of fish and molluscs harvested from aquaculture rose from 10 to 26 million tonnes (New 1999). The culture of bivalves has been particularly successful, with more than 85% of the total harvest of mussels and oysters being produced by aquaculture (New 1999).

In the South Pacific, bivalve aquaculture has followed global trends and production has increased significantly in the last 15 years. The greenshell® mussel (*Perna canaliculus*) is the most important edible bivalve species grown in the region and accounts for c. 80% of the total aquaculture harvest, by volume (FAO 2001, Fishstat+ Database).

P. canaliculus was formerly known as the green-lipped mussel. In the early 1980s the common name was changed to the greenshell® mussel and registered as a trademark. This gave the New Zealand mussel industry the exclusive right to the name. It also prevented other countries such as Brazil, India, Vietnam, Thailand, and the Philippines, which also exported green-lipped mussels (*Perna* spp.), from benefiting from the marketing of greenshell® mussels.

P. canaliculus is an excellent example of a species that was over-exploited in the wild and has subsequently become a highly valuable aquaculture crop. Landings of *P. canaliculus* from dredge fisheries in New Zealand peaked, in 1961, at more than 2000 tonnes (Greenway 1969, Reid 1969, Flaws 1975). Between the 1960s and 80s most of the wild fisheries collapsed and by 1992 less than ten tonnes of mussels were landed (Greenway 1969, Anon 1993). Experimental mussel farms were established in 1965 to compensate for declining catches (Greenway 1969). After a slow start, production increased rapidly through the 1980s and 90s. By 2001, 2500 ha of mussel farms were producing approximately 70,000 tonnes of mussels per annum (Lupi

2001). Production is likely to continue to increase significantly as an additional 7,735 ha of farms have been proposed for further development in the Marlborough Sounds area alone (Ministry for the Environment Marine Farm Database 2001).

Historically, mussel farming has been restricted to bays with minimal exposure to strong wind and waves. Seventy-five percent of farming currently occurs in the Marlborough Sounds, with the remainder occurring in sheltered areas in Golden Bay, Coromandel, and Stewart Island (Jefferies *et al.* 1999) (Figure 1.1). In addition to these traditional farming locations, large open-ocean farms, covering several thousand hectares, are being considered for development in areas including Pegasus Bay in Canterbury and the Firth of Thames in the Coromandel.

1.2 STUDY AREA

The Marlborough Sounds are a series of drowned river valleys located at the northern end of the South Island of New Zealand (41°S, 174°E), (Harris 1990) (Figure 1.1). The area provides a sheltered environment ideal for marine farming. The Marlborough Sounds consist of two main sounds: Queen Charlotte to the east and Pelorus to the west (Figure 1.2). More than 70% of the mussel farming occurs in Pelorus Sound, and for this reason it was chosen as the location to carry out this study.

Pelorus Sound extends approximately 50 km from the Pelorus River in the south to Cook Strait in the north. Along its length, numerous adjacent drowned valleys connect with the main channel to produce a complex system of bays and reaches. It is one of the most intensively studied tidal inlets in New Zealand. Over the past 30 years it has been the focus of research on sediment transfer (Carter 1976), spat settlement (Hayden 1995), mussel growth (Hickman 1979, Hickman & Illingworth 1980, Hickman *et al.* 1991), nutrients (Kaspar *et al.* 1985), phytoplankton dynamics (Gibbs 1993, Gibbs & Vant 1997), and shellfish sustainability (James & Ross 1996). It is classified as a coastal inlet with a long-residence-time (Heath 1976a): parcels of freshwater discharged from the Pelorus River during flood events take

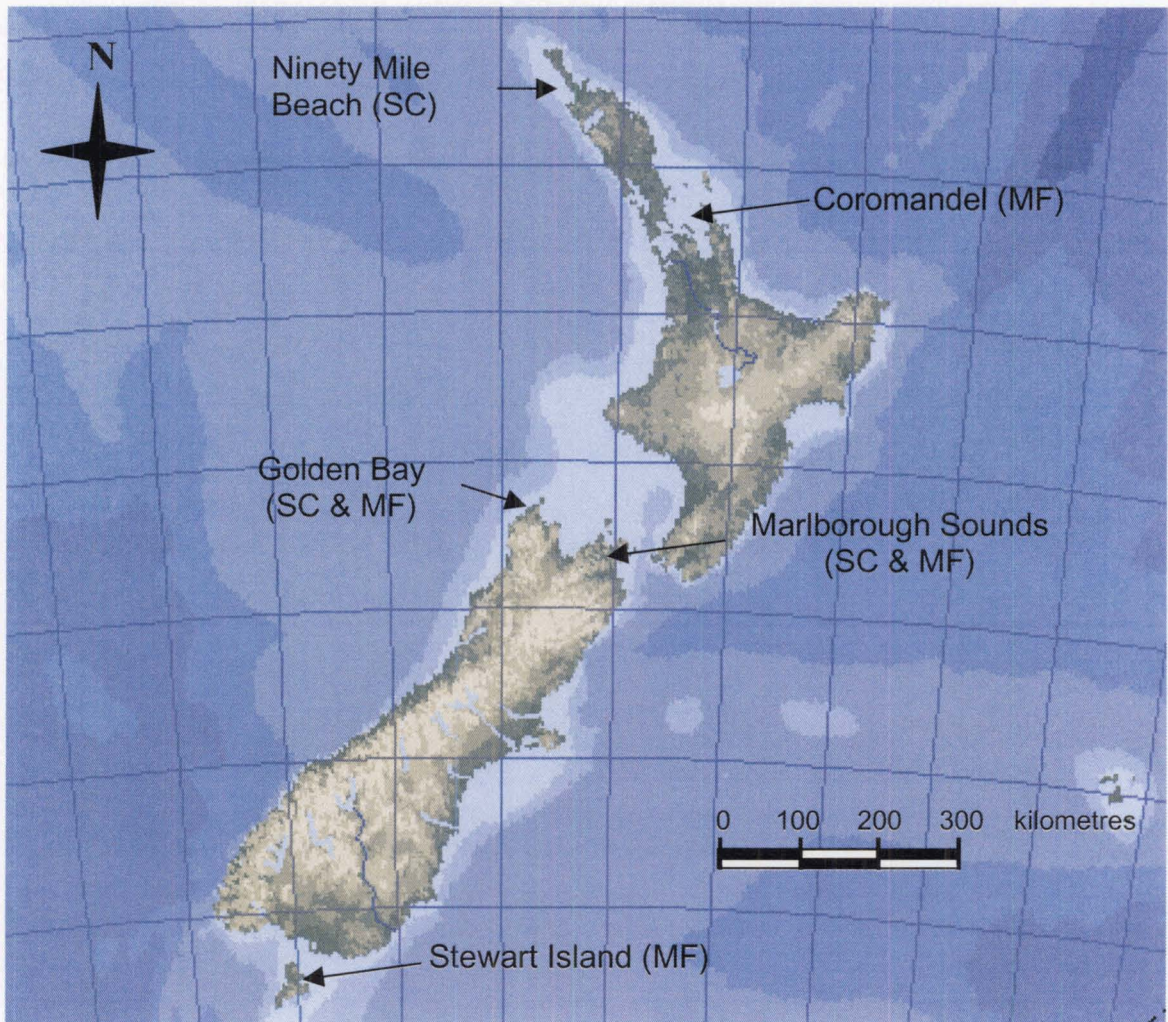


Figure 1.1. Locations of the main marine farming (MF) and spat catching (SC) sites in New Zealand.

approximately three weeks to pass through the Sound (Heath 1974). This is in part due to the large side arms that retain freshwater during flood events (Gibbs 1993). As in all estuarine waterways, salinities tend to increase towards the mouth, and from the surface downward (Heath 1976b). The salinity in the inner Sound (Kenepuru Sound) averages c. 28 ppt and in the outer Sound (Forsyth Bay) it is similar to the open ocean and averages c. 34 ppt (Sealord Shellfish Ltd. Unpublished data).

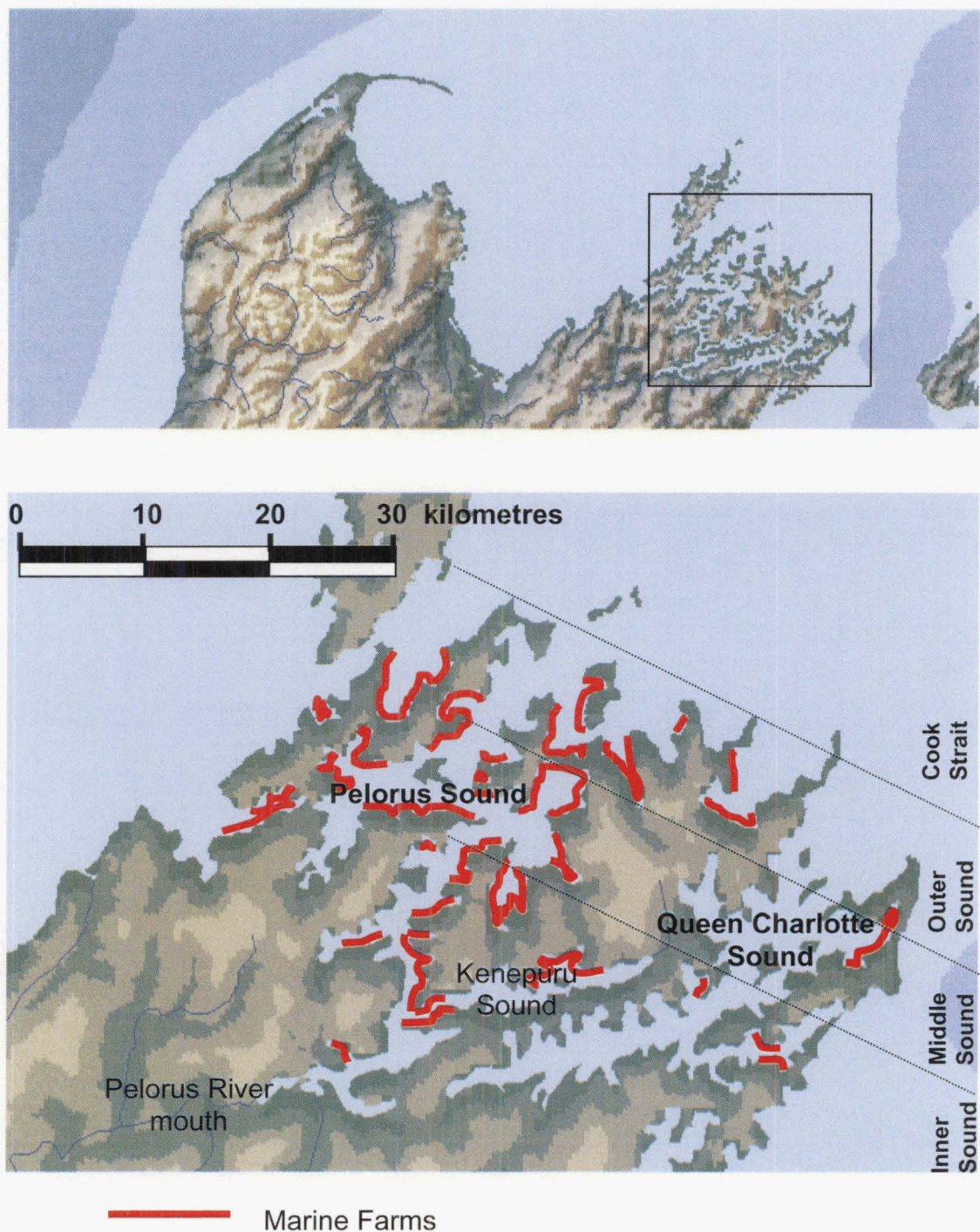


Figure 1.2. Location of marine farms in the Marlborough Sounds. For the purpose of this study, Pelorus Sound was divided into inner, middle, and outer culture areas.

When the Pelorus River floods, the salinity in the surface layer of the inner Sound can decline to less than 10 ppt. The inner Sound area also acts as a sediment trap and captures silt discharged from the Pelorus River during floods (Harris 1990). This sediment contributes to the high light attenuation in the inner Sound (Carter 1976, Vincent *et al.* 1989).

Pelorus Sound consists of three broad regions or areas (Hickman 1991): the inner Sound, which is strongly influenced by the Pelorus river; the outer Sound, which has oceanic influences from Cook Strait; and the middle Sound that is subjected to a combination of both influences. This classification system is used in the current study; the geographic range of each of the areas is shown in Figure 1.2.

1.3 GREENSHELL MUSSEL FARMING

Perna canaliculus is cultured using a longline system originally developed in Japan (Jefferies *et al.* 1999). The original method has been adapted to suit New Zealand's conditions and combined with increased mechanisation to produce a highly efficient farming system (Jenkins 1985). Most farms consist of between 5 and 10 individual longlines that occupy an area of c. 3 hectares (Figure 1.3). A longline is constructed of two 100-metre long backbone ropes joined by up to 50 plastic buoys (Figures 1.4a, b). Each longline is anchored to the sea floor at both ends. A continuous length of rope is lashed to the backbone longline and loops down to between 5 and 15 metres, depending on the depth of the site. Each loop of rope is called a dropper. Approximately 4000 metres of rope are suspended under a typical longline. As natural mussel spat settlement never occurs at ideal densities, spat are normally stripped from catching ropes and reseeded at lower densities twice during the growing cycle. Reseeding is usually done when mussels are c. 15 mm and c. 45 mm in shell length. Depending on their size, mussels are reseeded at densities of between 170 and 1000 mussels per metre. During this thinning process, spat are often reseeded on other farms. From initial spat capture, mussels usually take between 18 and 30 months to reach harvest size.

1.4 BIVALVE GROWTH

A wide range of morphometric variables have been used to quantify the growth of mussels (e.g., Hickman 1979). Shell length, meat weight, and condition are, however, of particular commercial interest. Length is important because it determines whether mussels are of a harvestable size; in the Marlborough Sounds mussels are usually harvested between 85 and 110 mm in length.



Figure 1.3. Two mussel farms in Elie Bay, Pelorus Sound.

Condition index is a measure of meat content, relative to size (Hickman *et al.* 1991). Condition and meat weight, at the time of harvest, are commercially important as they strongly influence the yield and financial return for farmers. The condition of farmed mussels in Pelorus Sound generally follows an annual cycle, with high values in autumn and spring and lower values in summer and winter (Hickman & Illingworth 1980, Hickman *et al.* 1991). Farmers report that condition and meat yields usually reach the lowest levels in mid-winter (June-August). If condition declines to very low levels, as it does most winters, mussels are not suitable to harvest. This was demonstrated in the winter of 1999 when the average monthly mussel harvest for the Marlborough Sounds fell from 5,013 tonnes in June to 2,880 tonnes in July (Figure 1.5). Several companies ceased harvesting and processing altogether, leading to the closure of factories and the lay-off of staff. The poor condition of mussels in mid-winter

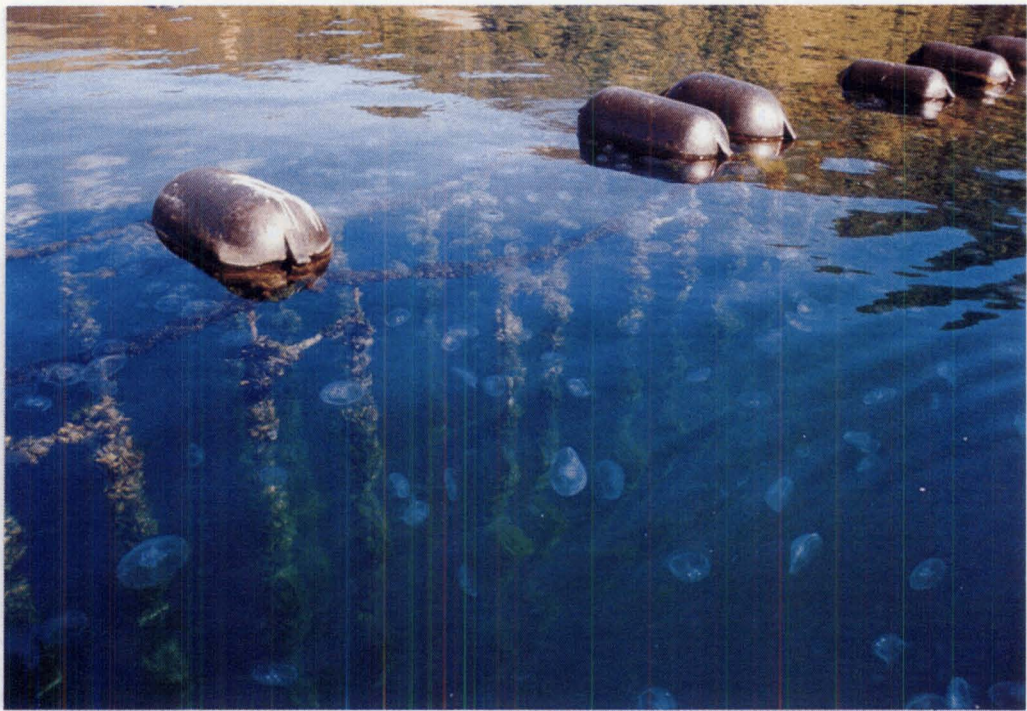
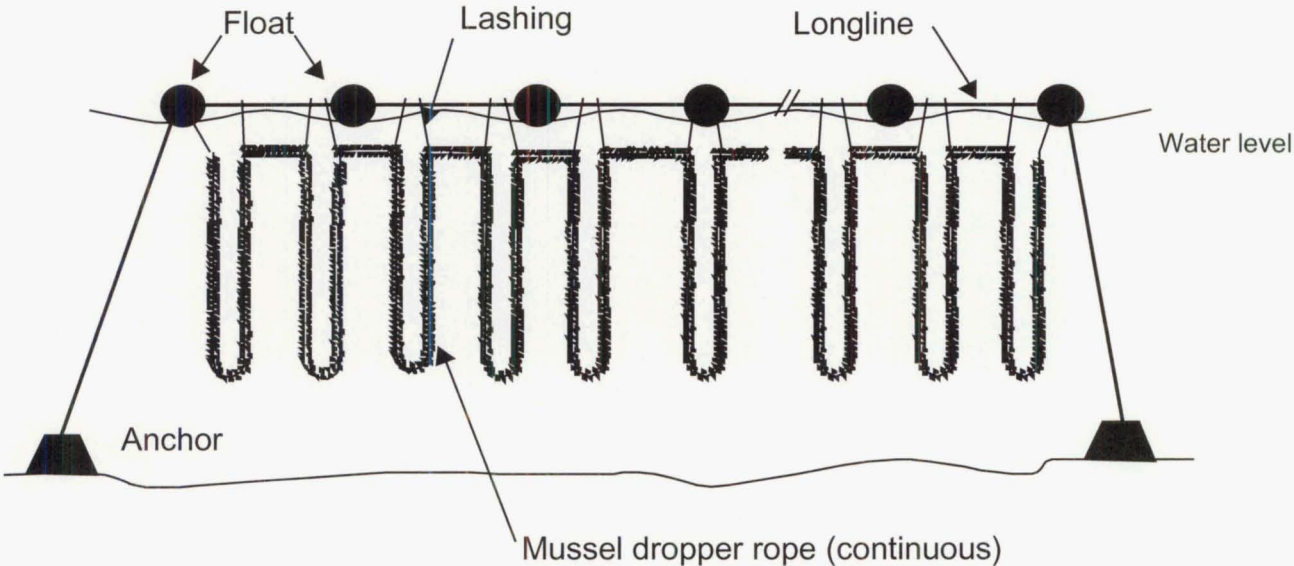


Figure 1.4. A typical commercial mussel longline. Mussels are grown on a continuous dropper rope that is lashed to the surface longline. Diagrammatic representation is not drawn to scale. Adapted from Ogilvie (2000).

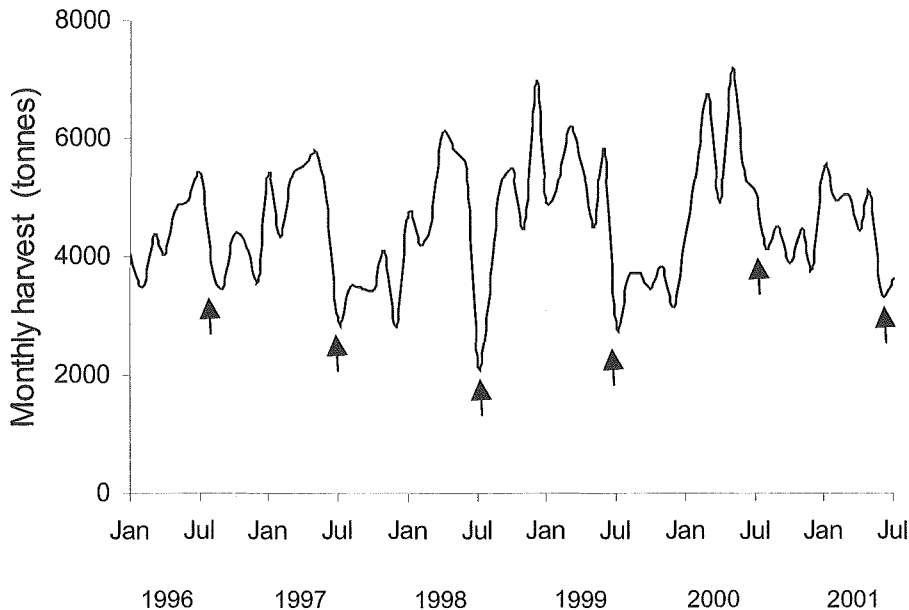


Figure 1.5. Monthly harvest tonnage for the Marlborough Sounds mussel industry between January 1996 and July 2001. Arrows show winter minima in harvest.

has important economic impacts on the mussel industry and nearby communities, and is one of the main problems facing the mussel industry in the Marlborough Sounds.

It is unclear what is causing the mid-winter decline in the condition of farmed mussels in the Marlborough Sounds. Overseas studies have suggested that the poor condition of bivalves in winter is usually due to reduced food levels (Ansell 1972, Hancock 1972). Phytoplankton is accepted as the most important food item for filter feeding bivalves (Bayne & Newell 1983, Rodhouse *et al.* 1985, Grant 1996). As a consequence, seasonal changes in phytoplankton abundance have the potential to influence bivalve growth and condition.

In the Marlborough Sounds, phytoplankton abundance follows a seasonal cycle (Ross *et al.* 1997, 1998a, b). The cycle begins with a low abundance in winter, when light levels are low and the water column is generally deeply mixed. This minimises the average amount of light that circulating phytoplankton cells are subjected to and retards growth. As the sea surface warms in spring, the water column becomes stratified, leading to a shallower mixed layer. This traps nutrients in

the well-lit surface waters and stimulates a spring bloom. The bloom is usually terminated at the start of summer by a combination of the depletion of nutrients and grazing by zooplankton (Harris 1978, Gibbs & Vant 1997). In autumn, the stratification that existed through summer breaks down and the surface waters are replenished with nutrients. This leads to a second phytoplankton bloom, generally smaller than the spring bloom. As light levels begin to decrease, phytoplankton abundance declines, again, to a winter minimum. This seasonal cycle suggests that the poor condition of farmed mussels in winter may be due to reduced food levels at this time.

Alternatively the poor condition of mussels in mid-winter may be due to spawning. Farmers in Pelorus Sound have reported that mussels sometimes spawn while being harvested in mid-winter. Histological examination of gonad tissue is generally regarded as the most reliable method for determining seasonal trends in reproduction (Seed & Suchanek 1992). Only one study has investigated the gonadal development of mussels in the Marlborough Sounds. Buchanan (1999) found that, in a wild intertidal population of *P. canaliculus*, the most mature reproductive states occurred in summer and autumn. It is not known whether the same reproductive cycle occurs in farmed mussels in Pelorus Sound. Both cultivation site and aerial exposure influence the condition and reproductive state of mussels (Piethers *et al.* 1980, Bayne *et al.* 1983, Borrero 1987), so it is possible that the reproductive cycle of the intertidal mussel population studied by Buchanan may not reflect the typical cycle found in farmed mussels. If the poor condition of farmed mussels in mid-winter is due to spawning, it is perplexing as no substantial spat settlement follows (Hayden & Kendrick 1992, Buchanan 1994).

1.5 THE DISTRIBUTION AND GENETICS OF *P. CANALICULUS*

P. canaliculus is endemic to New Zealand and grows in a range of habitats from the intertidal zone on rocky shorelines to depths of over 50 m on mud and sand (Morton & Miller 1973, Powell 1979, Buchanan 1994, Marsden & Weatherhead 1999). Despite being widely distributed around the North and South Islands of New Zealand, they tend to occur in geographically distinct populations (Jefferies 1999, Gardner 2000, Gardner & Thompson 2001). Factors that can control the distribution and abundance

of *P. canaliculus* include wave exposure (Morton & Miller 1973), the supply of larvae (Hayden 1995), the presence of suitable substrates for larvae to settle on (Buchanan 1994), predation (Hayden 1995), and food supply (Gardner 2000, Gardner & Thompson 2001).

The genetics of mussel populations have been intensively studied (e.g., Smith 1988, Sin *et al.* 1990, Gardner *et al.* 1996a, b, Apte & Gardner 2001). There is a general consensus that mussels are a genetically diverse group with significant variation occurring on macrogeographic, microgeographic, and temporal scales (Koehn *et al.* 1984, Koehn 1991). When mussel populations are separated by hundreds of kilometres (a macrogeographic scale), genetic differences may be maintained by reproductive isolation due to diverging water currents (Smith 1988), eddies that trap larvae (Gardner *et al.* 1996b), and separation by land masses (Koehn *et al.* 1984). Because mussels are broadcast spawners with a pelagic larval stage lasting 3-5 weeks (Utting & Spencer 1991, Buchanan 1999) genetic variation on microgeographic scales (i.e., metres to a few kilometres) appears to be due to the selective survival of specific genotypes in certain habitats (Gartner-Kepkay *et al.* 1983, Koehn 1984). Genetic differences between spat settling at the same site, but at different times (i.e., on a temporal scale), can be due to genetic drift, changes in selective forces through time, or sympatric populations of genetically dissimilar mussels having distinct and non-overlapping spawning seasons (Gosling & Wilkins 1985, Smith 1988).

Several studies have found genetic differences between populations of *P. canaliculus* in northern and southern New Zealand (Smith 1988, Sin *et al.* 1990, Gardner *et al.* 1996a, b). Smith proposed that these differences were due to genetic-physiological adaptations to different thermal environments. In addition he suggested that currents might partially isolate the populations by limiting the north-south movement of larvae. However, Apte and Gardner (2001) have disputed the existence of genetic differences between populations of *P. canaliculus*. In the largest genetic study that has been carried out on mussels in New Zealand, they found no significant variation among 30 populations of *P. canaliculus* around the coast of New Zealand.

Because of the contrasting results of these studies, the genetic structure of *P. canaliculus* populations in New Zealand has become controversial.

1.6 MUSSEL STOCKS

Although research has been directed towards the hatchery production of *P. canaliculus* spat, the Marlborough Sounds mussel industry is still completely reliant on the capture of wild spat to seed farms (Hayden 1995, Buchanan 1999). Mussel spat are collected from three locations: Golden Bay, the Marlborough Sounds, and Kaitaia (Figure 1.1). Two collection methods are used. At Ninety Mile Beach, near the town of Kaitaia in northern New Zealand, microscopic spat are washed ashore attached to a variety of seaweeds (Hickman 1976, 1982, 1987). This spat are collected, packed into boxes, and trucked 600 kilometres south to Marlborough Sounds where it is seeded onto mussel farms. The alternative collection method involves setting weighted ropes in Golden Bay and the Marlborough Sounds to capture settling spat (Pooley 1991). Approximately 80% of mussel spat used in the Marlborough Sounds originates from Kaitaia. Kaitaia spat are popular because they are cheap, easy to collect, and do not require farm space to collect.

In this thesis I have referred to mussels obtained from the three areas as Marlborough Sounds, Kaitaia, and Golden Bay stocks. Significant genetic differences have been identified between these stocks (Smith 1988, Gardner *et al.* 1996).

Multiple stocks are used by the mussel industry for two key reasons. First, it evens out the supply of spat. Spat settlement is highly variable on spatial and temporal scales (Hickman 1982 & 1987, Hayden and Kendrick 1992, Hayden 1995). If spat catching fails for several months very few harvest-sized mussels will be available 18-24 months later. The use of three catching sites (i.e., three stocks) minimises the impact of poor spat settlement at one or two of the sites.

The second reason for using multiple stocks is that many mussel farmers believe the stocks gain and lose condition at different times of the year, when grown in the Marlborough Sounds (Fox 1996). Anecdotal evidence suggests the two southern stocks (Marlborough Sounds and Golden Bay) remain in better condition over winter than mussels from Kaitaia.

If differences in condition cycles exist, it would be beneficial to harvest stocks at different times of the year, for example, harvesting the Golden Bay and Marlborough stocks during winter and the Kaitaia stock during summer. Potentially, this could improve the mean annual condition index of harvested mussels and minimise the impact of the mid-winter decline in condition (Figure 1.6). Increases in mean annual condition as small as 2% could be commercially relevant (Dr T. Osborne, pers. comm. April 1997). For example, improving the mean annual Cooked Weight Condition Index (CWI) of mussels harvested from 38% to 40% would increase the meat yield achieved by the Marlborough Sounds mussel industry by c. 1400 tonnes.¹ As harvest volumes continue to rise, any improvement in condition or growth that can be achieved will become even more relevant.

Several overseas studies have compared the growth of blue mussel (*Mytilus* spp) populations following transplantation to the same site (Dickie *et al.* 1984, Mallet *et al.* 1987, Mallet & Carver 1989, Kautsky *et al.* 1990, Fuentes *et al.* 1992, Fuentes *et al.* 1994, Stirling & Okumus 1994, Perez-Camacho *et al.* 1995). Although, in some of these studies the populations of mussels were only separated by a few kilometres (e.g., Mallet & Carver 1989, Perez-Camacho *et al.* 1995) the term stock was used to define the different populations. For this reason this definition of stock differs from the traditional one used by fishery scientists that assumes a degree of reproductive isolation (Ihssen 1981).

The growth of *Mytilus* stocks has been found to vary by as much as 130% at some sites (Perez-Camacho *et al.* 1995)(Table 1.1). It is unclear, however, whether these differences are true stock effects (i.e., genetically mediated) or are an artefact of the different environments that the mussel stocks were subjected to before they were transplanted.

If the differences in growth are genetically mediated, they are likely to be a consequence of selective processes in the home environments of the mussel stocks. Several studies have demonstrated that water temperature and salinity can exert a strong selective force in marine organisms such as mussels (Boyer 1974, Milkman & Koehn 1977, Lassen & Turano 1978, Hilbish & Koehn 1985, Gardner & Palmer 1998).

¹ Based on the 1999 harvest of 60,000 tonnes.

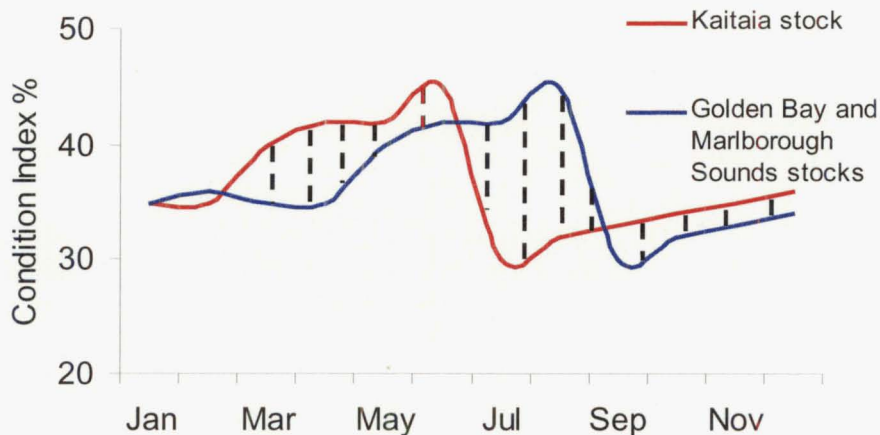


Figure 1.6. Hypothetical condition cycles of the Kaitaia stock, and the Golden Bay and Marlborough Sounds stocks in Pelorus Sound. The condition cycles are identical, but out of phase by two months. Dashed lines mark the periods during which increased yields could be achieved by selectively harvesting the stock with the better condition.

Genetically mediated variations in fitness could, therefore, account for the differences in growth observed between stocks in previous studies.

The environment that mussel stocks were exposed to before the studies also has the potential to influence the subsequent growth or condition of mussels. Although no research has been carried out on bivalves, in a range of animals including commercially important groups such as chickens, pigs, sheep, and salmonids, the prior growing environment can exert a strong influence on an animal's growth potential (Skilbrei 1990, Summers *et al.* 1990, Marais *et al.* 1991, Stamataris *et al.* 1991). The terms "catch up" or "compensatory growth" have been coined to describe the acceleration in growth that occurs when a period of growth retardation ends and favourable growing conditions (such as improved food levels) are restored. Therefore, if the early growing conditions of mussel stocks are not tightly controlled, it is possible that differences in growth could be due to physiological adaptations to the home environment rather than true stock effects (i.e., genetically mediated).

Although previous studies that compared the growth of *Mytilus* spp. stocks were important because they demonstrated that stock-related traits may occur in commercially cultivated mussels, all of the studies have two important shortcomings.

The first, and perhaps most important factor, is that the environment that the stocks were exposed to prior to sampling was not controlled. Stocks were collected from the wild at relatively large sizes (>15 mm) or grown at different sites for long periods before the experiments (Table 1.1). The second shortcoming is the absence of any replication at the stock level. It is unclear whether the same stock caught at different times will consistently exhibit the same growth traits. For traits to be commercially useful they must consistently occur in the stock.

In addition to these two major shortcomings, most of the studies were also carried out on a relatively small scale. Comparing the growth of several stocks at many sites through time is logistically difficult due to the large numbers of mussels that need to be sampled. Researchers minimised the size of the studies by running experiments for only short periods (Fuentes *et al.* 1992, Perez-Camacho *et al.* 1995), using relatively few experimental sites (Kautsky *et al.* 1990, Stirling & Okumus 1994, 1998), and increasing the duration between sampling (Mallet *et al.* 1987, Kautsky *et al.* 1990, Fuentes *et al.* 1992) (See Table 1.1 for a summary). The downside of these techniques is that some differences between stocks may not have been identified, particularly those involving the more dynamic variables such as meat weight and condition.

1.7 AIMS

This study uses a series of experiments to determine whether mussels obtained from Kaitaia, Golden Bay, and the Marlborough Sounds have different condition cycles and growth rates when grown in Pelorus Sound. Particular attention is paid to the mid-winter period when mussels are usually in poor condition. If differences in condition cycle occur between stocks, optimal stock combinations will be considered.

The core experiments closely control the early life history of mussels from a young age and small size to minimise the potential influence of different growing

environments. The study is of a design directly comparable with mussel farming practices, and involves the fortnightly sampling of three mussel stocks at six sites over two years. This approach increases the chance of detecting even subtle differences in growth between stocks and allows the application of results to farming practice. The growth of mussel stocks is compared in four separate trials, to determine whether traits identified in the trials are a consistent and predictable feature of the stocks.

The specific aims of the study are to determine:

1. Why mussels are in poor condition over winter;
2. Whether different mussel stocks have different growth rates and condition cycles when they are grown at the same location;
3. Whether traits associated with stocks occur regardless of the environment they are exposed to early in life, or the timing of spat capture;
4. Whether certain stocks of mussels grow better in particular areas of Pelorus Sound;
5. Whether differences in growth between stocks are significant when compared to spatial and temporal factors;
6. How the knowledge gained in this study can be used to increase yields in harvested mussels.

Table 1.1. Summary of published studies on the comparative growth of mussel stocks.

Authors	Species	Number of stocks	Number of sites	Maximum and minimum separation of stocks (km)	Initial spat size (mm)	Sampling frequency (months)	Duration of study (months)	Maximum difference in growth between stocks (%)
Dickie <i>et al.</i> (1984)	<i>M. edulis</i>	3	3	c. 210, <10	50	Monthly	24	<ul style="list-style-type: none"> • Length (36%)
Mallet <i>et al.</i> (1987)	<i>M. edulis</i>	11	9	c. 300, <10	15	0 & 6	6	<ul style="list-style-type: none"> • Length (78 %) • Dry weight (125%)
Mallet & Carver (1989)	<i>M. edulis</i>	11	9	c. 270, <10	26	0, 6, 9, 11 & 14	14	<ul style="list-style-type: none"> • Length (19%) • Dry weight (95%)
Kautsky <i>et al.</i> (1990)	<i>M. edulis</i>	2	2	c. 800	20	0, 9, 12, 13	13	<ul style="list-style-type: none"> • Length (10%)
Fuentes <i>et al.</i> (1992)	<i>M. galloprovincialis</i>	4	3	c. 30, 15	20	0 & 3	3	<ul style="list-style-type: none"> • Length (30%)
Fuentes <i>et al.</i> (1994)	<i>M. edulis</i>	4	3	c. 35 , <10	20	0, 4, 8 & 12	12	<ul style="list-style-type: none"> • Length (10%)
Stirling & Okumus (1994)	<i>M. edulis</i>	2	2	c. 60	26	Monthly	13	<ul style="list-style-type: none"> • Length (5%) • Live weight (20%) • Wet meat weight (6%) • Dry weight (70%)
Perez-Camacho <i>et al.</i> (1995)	<i>M. galloprovincialis</i>	3	3	c. 35, <10	25	0, 1 & 3	3	<ul style="list-style-type: none"> • Length (56%) • Live weight (130%)
Stirling & Okumus (1998)	<i>M. edulis</i>	2	2	c. 60	26	Monthly	12	<ul style="list-style-type: none"> • Condition index (40%) • Dry weight (70%)

Chapter 2

General Methods

2.1 INTRODUCTION

This chapter describes the general experimental design, the layout of experiments within the study sites, the sampling methods, and the data analysis techniques used in this thesis. More specific methods sections are included in each of the subsequent chapters.

2.2 GENERAL EXPERIMENTAL DESIGN

Mussels are among the most intensively studied of all marine organisms. From the several hundred studies that have been done on farmed mussels it is clear that many factors have the potential to influence their growth. Growth rates vary with time (Page & Hubbard 1987), between locations on both macro and micro geographic scales (Fuentes *et al.* 1994), between mussel stocks (Mallet *et al.* 1987), and possibly within mussel stocks caught at different times (e.g., in different spat catching seasons) (Gosling and Wilkins 1985). Although many of these factors have been studied individually or in association with one or two other factors, the influences of time, location, stock, and season of spat capture have never been studied on a large scale within a single experimental design. The reason is that such an experiment would be both time consuming and logistically challenging. From both a scientific and commercial perspective, however, there is a strong rationale to design and implement such a study. A hierarchical and orthogonal (i.e. balanced) experiment would allow variation to be partitioned in the experimental model between the factors (and their interactions) that influence growth. This would identify the most important factors influencing growth and allow subsequent research and/or commercial production to be directed towards them. The manipulation of factors that have the greatest influence on mussel growth has the potential to lead to significant increases in farm production.

In this thesis the growth of *P. canaliculus* was investigated in two large-scale studies. The first study (Chapter 3) ran between November 1997 and October 1998 and the second study (Chapter 4) ran between August 1998 and October 1999. The first study was set up to run until mussels in the second study were large enough to sample (c. 80 mm). The studies differed in two important ways.

The first difference related to the environment that the stocks were exposed to prior to sampling. In the first study, adult (60 mm+) mussel stocks were collected from different commercial mussel farms, and were therefore exposed to different environments prior to being moved to the study sites. This methodology reflected how mussel stocks are normally managed on commercial farms (i.e., they are moved between farms). This first study was done to determine whether differences in growth can occur between mussel stocks subjected to normal farm management practices.

If differences in growth were detected between stocks it would, however, raise the question “did the differences occur only because the stocks were exposed to different environments (farms) prior to being moved to the six study sites?” The second study was designed to address this issue. In the second study, mussel stocks were collected as newly settled spat (< 3.5 mm in length) and held at the same site, in Hallam Cove (Figure 2.1), until they were transferred to the six experimental sites. These stocks were exposed to the same environment from a few weeks of age until they were sampled, in some cases up to 30 months later. This methodology minimised, or eliminated, the possibility that any differences in growth between stocks were a consequence of the environment that stocks were exposed to before sampling began. Comparing the two studies would provide an insight to whether the environment that stocks are exposed to early in life can influence their subsequent growth potential.

The second key difference between the first and second studies was that in the second study the same mussel stocks were caught in the summer, autumn, and spring of 1997. This was done to determine whether the same stocks caught at different times (seasons) exhibit the same growth and condition traits.

Both studies were designed to be orthogonal and to allow variation to be partitioned between the factors (and their interactions) included in the experimental model.

2.2.1 Statistical design

The following factors were included in the experimental design of both studies: time, area, site, stock, and dropper. The additional factor of season of capture was included in the second study.

Time: Mussel growth varies through time. Condition is a particularly dynamic variable and, in Pelorus Sound, can change by up to 30% over a month (Hickman *et al.* 1991). It is also believed that the condition of the three stocks changes through time, with Golden Bay and Marlborough Sounds stocks being in higher condition than the Kaitaia stock over winter (Fox 1996). In order to detect any fine-scale temporal changes in the condition, sampling was carried out at fortnightly intervals.

Season (of capture): In the second study, attempts were made to catch mussel stocks from Golden Bay, Kaitaia, and the Marlborough Sounds in the summer, autumn, winter, and spring of 1997. Genetic variation can occur between mussels caught at different times of the year (Gosling & Wilkins 1985, Smith 1986). Therefore, it is possible that genetically mediated differences in growth might also exist between mussels caught in different seasons. This is the first study that has attempted to compare the growth of mussels (and stocks) caught in different seasons. Season of capture was not included as a factor in the first study.

Area: Mussels are farmed in Pelorus Sound from Kenepuru in the inner sound through to Anakoha in the outer sound (Figure 2.1). Both Cook Strait and the Pelorus River produce several important chemical and physical gradients along the length of the sound. Water that is dense, saline, and nitrogen-rich enters the sound from Cook Strait and fresh, low-density water enters from the Pelorus River (Bradford *et al.* 1987, Dupra, 2000). As a consequence, the waters of the inner, middle, and outer sound have different characteristics, which could influence growth (Table 2.1). A spatial scale of "area" was included in the experimental design to determine whether mussels (or stocks) grown in the inner, middle, and outer areas of Pelorus Sound have similar or dissimilar growth rates.

Site: Two experimental sites (mussel farms) were selected in each of the three areas of Pelorus Sound (Figure 2.1). Replicating sites allowed within area variation in growth to be quantified. It also provided information on whether the growth of mussels (or stocks) could be predicted according to the area in Pelorus Sound where they were located. The six experimental sites spanned the range of environments under which mussels are farmed in the Sound. Lower salinities, heavy sediment loads, and faster currents characterise inner sound sites while the outer sound sites have high salinities, low sediment loads and slower currents (Carter 1976, Heath 1976, Gibbs *et al.* 1991)(Table 2.1).

Stock: When feasible, three mussel stocks were grown at each experimental site. Using this design it was possible to determine whether stock had a significant influence on growth and whether any differences in growth were related to the site, area, or time at which the mussels were sampled.

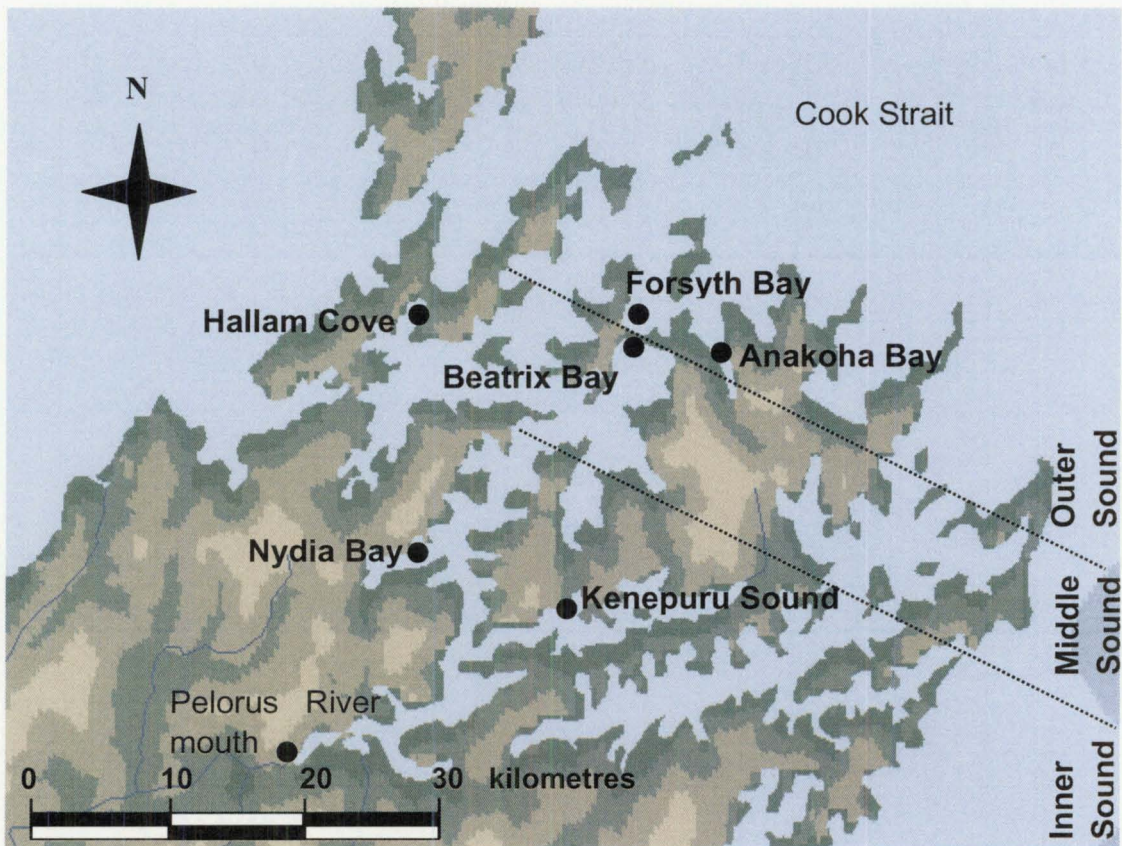


Figure 2.1. Location of study sites in Pelorus Sound. Kenepuru Sound and Nydia Bay are located in the inner area, Beatrix Bay and Hallam Cove are in the middle area, and Forsyth Bay and Anakoha Bay are in the outer area.

Dropper: Duplicate droppers of each stock were grown at each site to determine whether there was significant variation at the very lowest level within the experimental model. Duplicate droppers also guaranteed a surplus of mussels for the experiment; this reduced the percentage decline in mussel density during the experiments and ensured that if one dropper was lost the orthogonal design of the studies remained intact. Each fortnight, 20 mussels were collected from each duplicate dropper of each stock at each of the two sites within the three areas of Pelorus Sound (Figure 2.2).

The large scale of these studies ensured the findings would be directly applicable to the mussel industry in Pelorus Sound.

Table 2.1. Physical and biological characteristics of the study sites. Data were collected by Sealord Shellfish Ltd. at approximately fortnightly intervals between November 1996 and November 1997 (n=22). Temperatures, salinities, secchi readings, and chlorophyll values are averages of samples collected at 1 and 5 m. Ranges are included in square brackets. Current speeds were estimated by measuring the speed of neutrally buoyant objects on the outside of the farms. Standard errors are enclosed in parentheses.

Area	Site	Mean water temperature °C	Mean salinity (ppt)	Mean secchi disk (m)	Chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$)	Depth of site (m)	Surface current speed (cm s^{-1})
Inner	Kenepuru Sound	15.5 (0.6) [10.8-20.1]	28.6 (1.2) [14.5-34.4]	3.2 (0.3) [0.1-7]	1.9 (0.2) [0.1-3.8]	6	50
	Nydia Bay	Data not available				5	20-30
Middle	Beatrix Bay	15.2 (0.5) [11-19.5]	30.7 (0.8) [26.2-34.4]	8.1 (0.8) [0.6-16]	1.9 (0.2) [0.3-4.1]	15	<20
	Hallam Cove	15.4 (0.6) [10.8-19.5]	31.2 (0.4) [26.1-34]	8.1 (0.5) [3.2-12]	1.4 (0.2) [0.3-4.2]	25	<20
Outer	Forsyth Bay	14.6 (0.7) [12-18.5]	33.5 (0.5) [30.1-34.6]	5.4 (0.5) [2.9-9.5]	1.7 (0.2) [0.3-4.0]	26	<10
	Anakoha Bay	14.6 (0.5) [10.7-19.4]	33 (0.2) [28.2-32.4]	8.1 (0.5) [0.2-8.5]	1.7 (0.2) [0.2-5.8]	25	<20

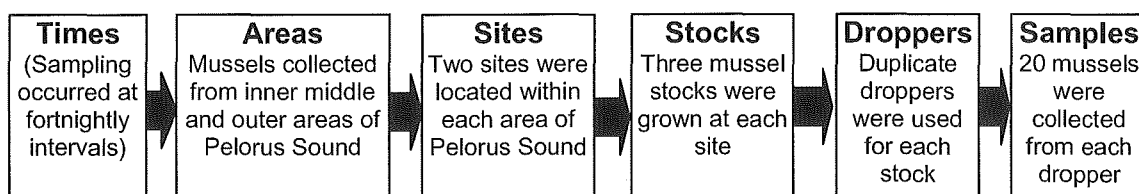


Figure 2.2. General design of the two growth trials used in Chapters 3 and 4. The additional factor of season of capture was included in the second study. Detailed schematic diagrams of the experimental designs are presented in the methods sections of each chapter.

2.3 LAYOUT OF EXPERIMENTS WITHIN THE STUDY SITES

On each of the six mussel farms, duplicate 5 metre droppers of each stock were hung on the end of the outermost longline (Figure 2.3) Each dropper was labelled with a PVC tag to identify the stock and season of capture. Anecdotal evidence suggested mussels have elevated growth rates in the top 0.5 metre of the water column. To eliminate this source of variability, droppers were suspended under 0.5 metre ropes (Figure 2.3). Half way along each dropper a length of rope was attached. This was used to lift the droppers from the water during sampling

(Figure 2.3 & 2.4). Droppers were spaced c. 0.75 metres apart. Duplicate droppers ensured a back-up dropper was available if one was lost.

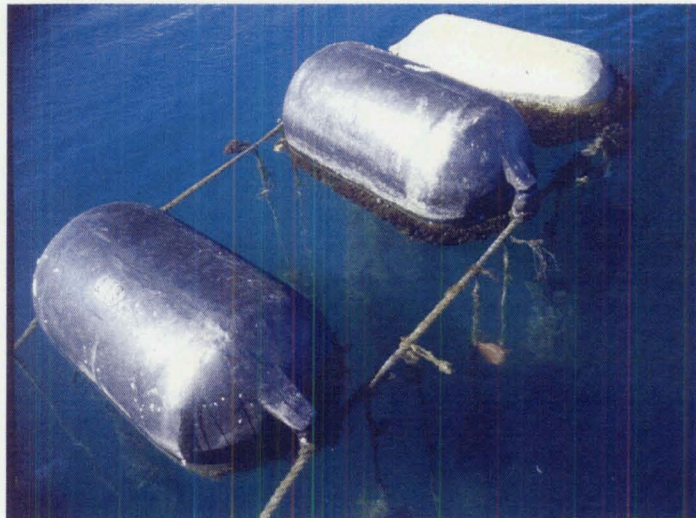
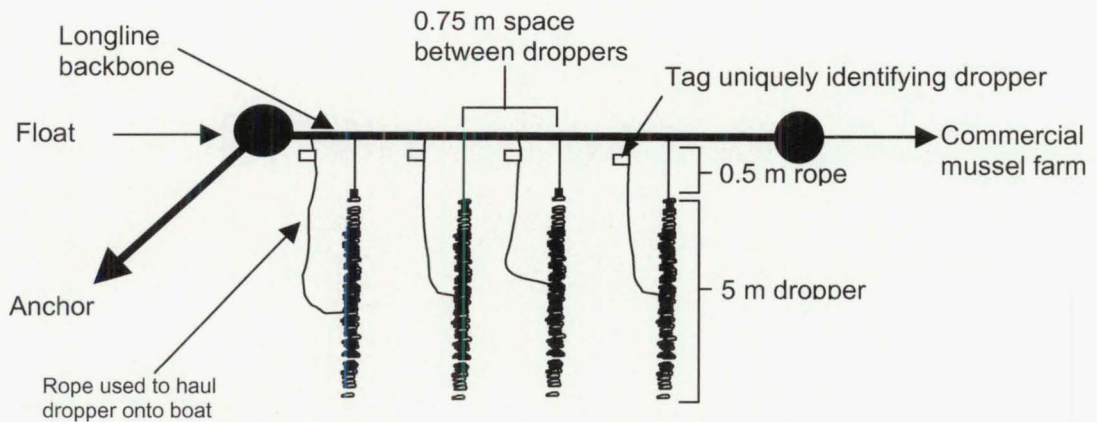


Figure 2.3. Experimental droppers hanging from the backbone of a mussel farm.

2.4 SAMPLING METHODS

2.4.1 Mussel samples

Typically, samples were collected at fortnightly intervals, with the actual collection of samples spanning three days. Occasionally, mechanical problems with the boat and bad weather disrupted sampling. The dates on which sampling began are given in the methods of Chapters 3 and 4.

Sealord Shellfish's 6.8 metre boat, *Mollusca*, was used for the fieldwork throughout the project. Modifications, including an additional winch and a stainless steel chute, were added to make it easier to haul mussels aboard the boat (Figure 2.4).



Figure 2.4. Attaching a rope to the middle of each dropper allowed the 5 m droppers to be hauled into a 3 m wide boat.

Five mussels were collected from four evenly spaced positions along each duplicate dropper. Each sample of 20 mussels was bagged and kept in a thermally insulated container out of direct sunlight until they were processed back at the Sealord laboratory at Elaine Bay. Samples were labelled with the dropper, site, and area from which they were obtained. In the second experiment, the season in which the spat were initially caught was also recorded. The shell length, total cooked weight, and cooked meat weight were recorded for each mussel. Mussels were cooked using the standard commercial cooking process of immersing mussels in seawater at 95°C for 5 minutes. Shell and meat weights were measured to the nearest ± 0.1 g and length to the nearest mm. The total cooked weight is the combined cooked weight of the shell and meat.

A Cooked Weight Condition Index (CWI), $CWI = \text{Cooked Meat Weight} / \text{Total Cooked Weight} \times 100$, was calculated for each mussel (modified from Hickman & Illingworth 1980). The CWI is different from the Green Weight Index ($GWI = \text{Cooked Meat} / \text{Total Live Weight}$) used by much of the mussel industry. The GWI was not used in this study as the amount of water contained within a

mussel depends on whether shell gaping has occurred. As a consequence the GWI is less precise than the CWI.

All measurements were dictated onto tape and transcribed into an Access® database (Microsoft® Inc, USA) after the fieldwork was completed each fortnight.

2.4.2 Mussel densities

At the completion of each experiment, the density of mussels on each experimental dropper was estimated. This was achieved by dividing the total weight of mussels on the dropper by the mean weight of the mussels, and then dividing the estimated total number of mussels by the length of the dropper (5 metre droppers were used).

2.4.3 Assessment of reproductive state

The reproductive state and CWI of each mussel was recorded to establish whether there was a link between the two variables. Female gonads were staged according to gonad colour and follicle development (Buchanan 1999). Only female mussels were staged as there is a high degree of synchrony between the sexes, and females are easier to stage due to the pink gamete colouration (Buchanan 1999). Each time mussels were sampled, the number of female mussels at each reproductive stage was recorded.

In the first study (Chapter 3) the classification system divided mussels into three stages (Table 2.2a). In the second study (Chapter 4), the classification was expanded to four stages to reflect the system published by Buchanan (1999) (Table 2.2b).

2.4.4 Environmental data

Water samples were collected immediately prior to mussel samples to avoid the contamination of chlorophyll *a* samples with benthic diatoms and fragments of macrophytes dislodged from the mussel droppers. Data were collected as a part of a large environmental monitoring program that has been operated by Sealord Shellfish Ltd. since 1995. As a part of this program water samples were collected using two methods. At all of the study sites, except Forsyth Bay, 2-litre water samples were collected at depths of 1 and 5 metres

Table 2.2a & b. Descriptions of the visual grading systems used to assess the reproductive state of female mussels in (a) Chapter 3 and (b) Chapter 4. Grading systems were adapted from Buchanan (1999).

(a)

Visual grade	Description
Stage one	Very pale orange colouration of gonads. Immature gonads.
Stage two	Light orange coloured gonads. Gonads maturing.
Stage three	Gonads are fully matured and bright orange in colouration. Spawning ducts are clear and easy to see.

(b)

Visual grade	Description
Stage one	Pale colouration of gonads. Follicles observed on < 30% of gonad. Immature gonads.
Stage two	Light orange coloured gonads. Follicles observed on < 50% of gonad. Gonads at early stage of maturation
Stage three	Darker orange coloured gonads. Follicles observed on < 75% of gonad. Gonads becoming well developed.
Stage four	Gonads a bright orange to pink. Follicles observed on >75% of gonad. Fully mature gonads.

using a Van Dorn sampler (Greenberg *et al.* 1992). At Forsyth Bay, an integrated sampler (Andersson 1996) was used to obtain a water sample between the surface and 20 metres. At each of the six sites, a sub-sample of water was transferred to a 1-litre opaque bottle. These samples were then stored in a thermally insulated container and transported back to the laboratory. Water temperature (± 0.1 °C) and salinity (± 0.1 ppt) was measured in the remainder of the sample using a CTD meter (YSI instruments, USA).

Once back at the laboratory, the 1-litre water samples were filtered using GF/C glass fibre filters and frozen. At regular intervals, batches of samples were sent to the NIWA Hamilton Chemistry laboratory for chlorophyll *a* analysis. Chlorophyll *a* levels were determined using the methods described by Pridmore (1983).

2.5 DATA ANALYSIS

Due to the large volume of data collected during the study (c. 460,000 entries), all data were stored and managed in an Access® relational database (Microsoft ® Inc., USA) prior to statistical analysis in Statistica® (StatSoft ® Inc., USA). The orthogonal and hierarchical design of the experiments allowed analysis

Chapter 3

The influence of stock, time of harvest,
and culture area on the condition and shell growth of farmed
Perna canaliculus

3.1 INTRODUCTION

Mussels are well suited to intensive aquaculture (Velez & Epifanio 1981, Walter 1982, Jenkins 1985, Chalermwat & Lutz 1989, Wanninayake & Sarath-Kumara 1989, Perez-Camacho 1991). They are robust and grow in a wide range of environments (Garden 1998, Marsden & Weatherhead 1999), are not badly affected by parasites or diseases (Hickman 1978, Pregonzer 1983, Jeffs 1999), and have high growth rates in suspended culture (Hickman 1979, Rivonker 1993). These attributes have made mussel farming highly efficient and, at times, very profitable. As a consequence mussel farming has developed rapidly and now occurs in more than 30 countries from New Zealand to Norway (Jenkins 1985, Nysaether 1988, FAO statistics 1993).

Currently, farming is restricted to sheltered areas such as the rias of northern Spain, lochs of Scotland, fjords of Norway, and sounds of New Zealand and Canada (Aiken 1984, Kleppe 1985, Contreras-Tebar 1987, Stirling & Okumus 1994, Jeffs *et al.* 1999). Although these locations are ideal for growing mussels, most have an insufficient or an unreliable supply of spat (Meredyth-Young & Jenkins 1980, Hickman 1987, Edwards 1997).

Many processes can influence the abundance and recruitment of sessile marine organisms, such as mussel spat (Dayton 1971, Connell 1975, Menge & Sutherland 1976, Menge 1991). The supply of larvae, the active migration of juveniles, and predation by fish all contribute to variations in the supply of *Perna* spat (Buchanan 1994, Hayden 1995). Mussel hatcheries have the potential to eliminate the need to collect wild spat. At present, however, it is both difficult and expensive to produce mussels commercially in a hatchery (Falmagne 1983, S. Buchanan pers. comm. February 1999). Because spat settlement varies between sites and through time (Bernard & Judson 1991, Hayden & Kendrick 1992, Fuentes & Molares 1994), most mussel industries have attempted to find multiple sites to collect spat (e.g. Hayden & Kendrick 1992). All of the large mussel industries of the world, including those in Spain, Chile, Norway, and New Zealand now rely on the capture of wild spat from several different locations (Contreras-Tebar 1987, Hickman 1987, Figueras 1990, Dijkema 1992).

Mussel farmers in the Marlborough Sounds have suggested that spat collected from different locations (i.e., stocks) have different growth rates when grown at the same site (Fox 1996). Research on *Mytilus* spp. supports these anecdotal observations (see General Introduction). Mussel farmers in the Marlborough Sounds believe that mussel stocks from Golden Bay and Marlborough Sounds are usually in better condition than the Kaitaia stock over winter. If this is correct, the selective harvesting of stocks at different times of the year could help increase the average annual yield and minimise the impact of the mid-winter decline in condition.

This chapter aims to determine:

1. Why mussels are in poor condition over winter;
2. Whether mussel stocks that have been exposed to commercial farming practices have different condition cycles and shell growth rates when they are grown at the same location;
3. Whether differences in growth between stocks are significant when compared to spatial and temporal factors.

If differences in growth exist between *P. canaliculus* stocks, ideally the differences need to occur regardless of the environment to which mussels have previously been exposed. This is relevant because mussels are almost invariably moved between farms and exposed to different environments during the normal commercial farming cycle. This study uses mussel stocks that were exposed to different environments (mussel farms) before the experiment. The results of this study will be compared to those of the next study (Chapter 4) in which the environment that mussel stocks were exposed to was closely controlled from initial capture through to sampling. Comparing the studies will provide an insight to whether the early growing environment can influence the subsequent growth potential of mussels.

3.2 METHODS

3.2.1 Selection and collection of mussel stocks

Sealord Shellfish Ltd. stores information on the location, age, density, and origin of all the mussels grown on its farms in a crop-management database. This database was examined to identify and locate Golden Bay, Kaitaia, and Marlborough Sounds stocks of a similar shell length, density, and age. An exact 3-way match between stocks proved to be impossible. Therefore, a pair of “small” Kaitaia and Golden Bay stocks and a pair of “large” Kaitaia and Marlborough Sounds stocks were selected for comparison (Table 3.1). The two small stocks (Golden Bay and Kaitaia) had mean lengths of c. 64 mm and the two large stocks (Marlborough Sounds and Kaitaia) had mean lengths of c. 73 mm. The Golden Bay and Marlborough Sounds stocks were compared against the Kaitaia stock because the Kaitaia stock is the standard stock used by 80% of the mussel industry (Lupi 2001). Mussels in each pair were of similar age, density (170-180 mussels m^{-1}), and were obtained from the same embayment (Table 3.1).

P. canaliculus are commercially harvested when they are between 80 and 110 millimetres in shell length. To ensure the experimental findings were applicable to mussel farming, the stocks were selected so they would be within this size range when they were sampled between November 1997 and October 1998.

The long commercial droppers on which the mussel stocks were growing were cut into 5 m droppers (Figure 2.3 General Methods). Approximately 850 mussels were on each dropper. In August 1997 duplicate droppers of each stock were transferred to the six experimental sites. In total, approximately 40,000 mussels were transferred to the six study sites. A description of the study sites, the layout of the droppers within the sites, the sampling protocols, and the data analysis techniques are outlined in the General Methods (Sections 2.2-2.5). The mussel stocks were left in place at the experimental sites for 3 months until sampling began.

At fortnightly intervals, from November 1997 onwards, 20 mussels were collected from each duplicate dropper of each stock at the six sites (two sites in each of the three areas). This sampling continued until October 1998. A schematic diagram

of the experimental design, including the dates when sampling occurred is presented in Figure 3.1.

3.3.2 Collection of environmental data

Several environmental variables were recorded to establish whether links could be made between the environment and mussel growth. Water temperature, salinity, and chlorophyll *a* were recorded at each site when mussels were collected (Section 2.4.4 of the General Methods). Day lengths were obtained from sunrise and sunset tables for Nelson (New Zealand Nautical Almanac 1997-2000).

Table 3.1. The size, density, age, and origin of the mussel stocks.

Stock	Size class	Initial length \pm standard error (mm)	Embayment from which mussels were obtained	Date of spat capture
Golden Bay (GS)	small	63.7 ± 0.8	Anakoha	Apr 1996
Kaitaia (KS)	small	64.7 ± 0.8	Anakoha	Apr 1996
Kaitaia (KL)	large	73.0 ± 1.0	Beatrix	Jan 1996
Marlborough Sounds (ML)	large	72.4 ± 1.0	Beatrix	Feb 1996

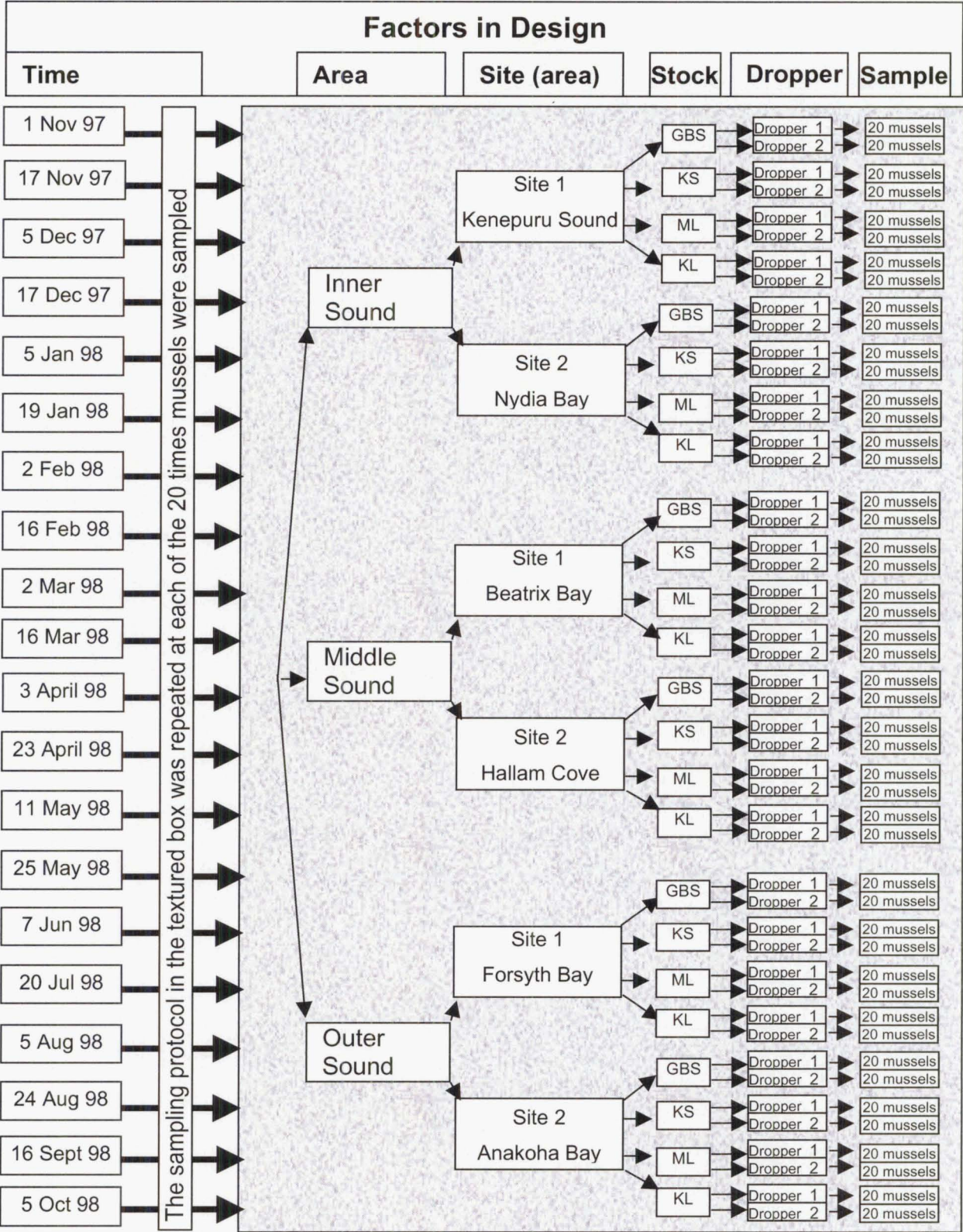


Figure 3.1. Hierarchical model of the experimental design used in Chapter 3. Samples were collected 20 times between 1 November 1997 and 5 October 1998. Each fortnight 20 mussels were collected from each duplicate dropper for each stock, at each site, in each area. GBS = Golden Bay small, KS = Kaitaia small, ML = Marlborough Sounds large, and KL = Kaitaia large.

3.3 RESULTS

3.3.1 Influence of stock, time, and area on mussel condition

The factors influencing the condition of mussels in Pelorus Sound between November 1997 and October 1998 were tested using an analysis of variance (ANOVA). Preliminary analyses showed that condition indices were comparable between mussels of different sizes (Appendix 2). There was also no significant dropper effect (Appendix 3), so data from replicate droppers were pooled.

In this section, each of the statistically significant factors and interactions are discussed in the hierarchical order in which they occur in the ANOVA model (Table 3.2). The significant factors are Time, Site (area), Stock, Time \times area, Time \times site (area), Time \times stock, Site (area) \times stock, and Time \times site (area) \times stock (Table 3.2).

It is important to note that the highest order interaction (Time \times site (area) \times stock) in the model was significant and that some of the significant single factors (e.g. Time) would contribute unequally to the higher order interactions.

Overall, the factors (and interactions) examined in the model explained 57% of the total variation in condition. A further 43% of the variation was not explained by the model (i.e., residual SS / total SS = 0.43).

Table 3.2. ANOVA of factors that may influence the condition of mussels. Condition is the dependent factor and time, area, site (area), and stock are independent factors. Time, area, and stock are fixed and site (area) is random and nested within area. The percentage of the variation accounted for by each factor (and interaction) is presented in the % variation column (calculated as the SS for each factor / Σ SS of all factors in model). *** = $p < 0.001$.

Factor	DF effect	MS effect	SS	F-value	P-value	% variation
Time	19	4921	93494	6.2	0.00***	15.2
Area	2	12249	24497	1.8	0.30	3.9
Site (area)	3	6645	19934	466.1	0.00***	3.2
Stock	3	4747	14241	20.9	0.00***	2.3
Time \times area	38	2469	93834	3.1	0.00***	15.2
Time \times site (area)	57	790	45040	55.4	0.00***	7.3
Time \times stock	57	261	14852	2.0	0.00***	2.4
Area \times stock	6	400	2399	1.8	0.21	0.3
Site (area) \times stock	9	227	2047	16.0	0.00***	0.3
Time \times area \times stock	114	134	15219	1.0	0.43	2.4
Time \times site (area) \times stock	171	130	22204	9.1	0.00***	3.6
Residual	18720	14	266872			43.4
Total	19199	32985	614634			100

ANOVA – Main effects

Time: Time accounted for 15% of the total variation in condition. Condition was consistently high between November 1997 and June 1998 (Figure 3.2). Between June and July 1998 condition declined from c. 38 to 31%. This mid-winter decline in condition was the most pronounced feature of the condition cycle during the study. From July onwards condition generally improved and reached c. 35% by the end of the study in October.

The mid-winter decline in condition coincided with a shift from most mussels (c. 80%) being either mature or in a process of maturing to the majority of mussels (> 90%) being immature. This indicated that a significant spawning event was responsible for the decline in condition in mid-winter. The condition index was correlated with both day length and water temperature but not salinity or chlorophyll a (Table 3.3). The lowest condition indices coincided with short day lengths and low water temperatures (Figure 3.3).

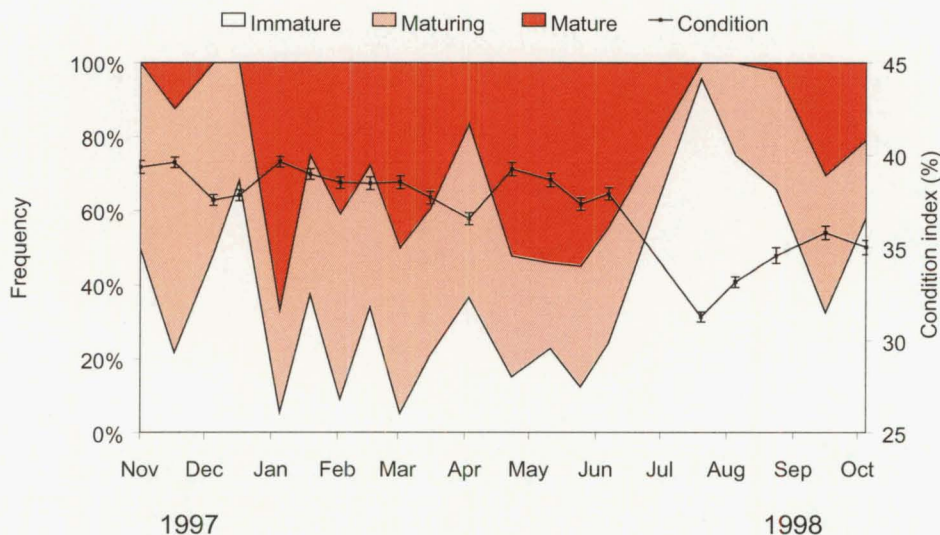


Figure 3.2. Changes in condition index and reproductive state. Full descriptions of each reproductive stage are given in Table 2.1 in the General Methods. Data were grouped for all six sites and all stocks. Bars = \pm 95% confidence intervals.

Table 3.3. Spearman's Rank Correlation coefficients (r-values) between mussel condition and water temperature, day length, salinity, and chlorophyll a. Significant relationships are in bold (n= 20).

	Temperature	Day length	Salinity	Chlorophyll a
Condition	0.49 (p=0.03)	0.47 (p=0.01)	0.27 (p= 0.10)	0.09 (p=0.65)

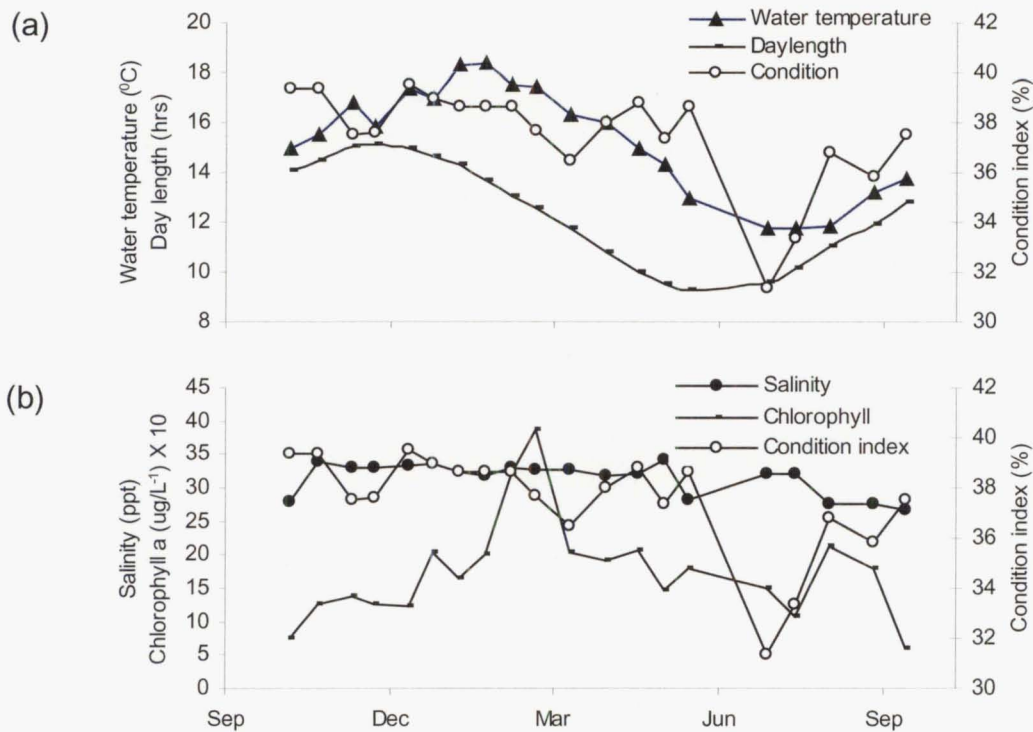


Figure 3.3. Seasonal changes in water temperature, day length, salinity, chlorophyll and mussel condition in Pelorus Sound. Day lengths were obtained from sunrise and sunset tables for Nelson (New Zealand Nautical Almanac 1997-2000). Water temperatures were recorded at fortnightly intervals at each of the six experimental sites and averaged.

Site (area): Although there was no significant difference in condition between culture areas (inner, middle and outer), a significant difference occurred between sites within these areas. The largest variation in mean condition between sites within areas occurred in the middle (3.3%) and outer sound (1.5%); only minor differences occurred in the inner sound (0.2%)(Figure 3.4). Site(area) accounted for 3% of the variation in condition.

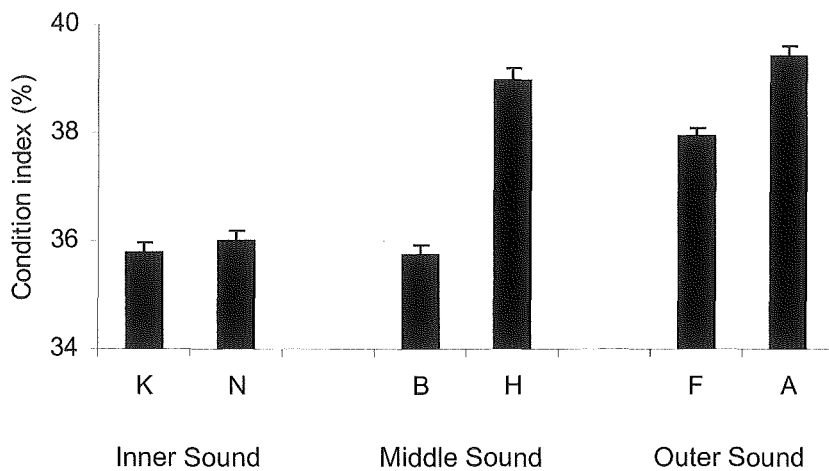


Figure 3.4. Mean condition indices of mussels at each study site between November 1997 and October 1998. K = Kenepuru Sound, N = Nydia Bay, B = Beatrix Bay, H = Hallam Cove, F = Forsyth Bay, A = Anakoha Bay. Sites have been grouped by area. Bars = \pm 95% confidence intervals.

Stock: Stock accounted for 2% of the variation in condition. The Golden Bay stock had the lowest condition index with a mean of 36.0% and the Marlborough Sounds stock had the highest condition index with a mean of 38.5% (Figure 3.5). The large and small size classes of the Kaitaia stock had a mean condition index of 37.5%.

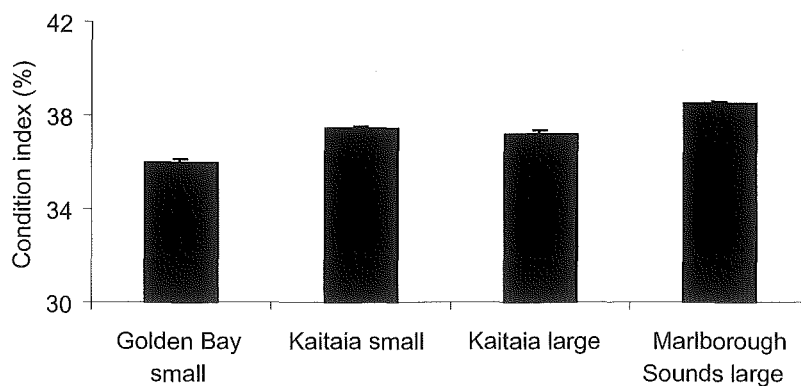


Figure 3.5. Mean condition index of each mussel stock between November 1997 and October 1998. Bars = \pm 95% confidence intervals.

ANOVA - Interactions

Time × area: Time × area accounted for 15% of the variation in condition. The interaction indicated that the differences in condition, between the three areas of Pelorus Sound, varied over time (Figure 3.6). This was particularly evident following the mid-winter decline in condition. Mussels grown in the middle sound improved in condition (from c. 30% to 40%) in the following weeks, while the condition of those in the inner and outer sound did not.

Time × site (area): Time × site (area) accounted for 7% of the variation in condition. This interaction demonstrated that the difference in condition, between sites within areas of Pelorus Sound, varied over time (Figure 3.6). For example in the first half of the study, in the middle sounds, the condition indices of mussels in Beatrix Bay were lower than mussels in Hallam Cove. Later in the study, however, the condition of the mussels at the two sites was similar. Although the condition of mussels varied between sites within areas for most of the year, there was minimal variation between any of the six sites in mid-winter (2% range in July).

Time × stock: Time × stock accounted for 2% of the variation in condition. The mussel stocks exhibited small, but statistically significant, differences in condition cycles (Figure 3.7). Between January and June 1998 the condition of the Golden Bay stock was lower (up to 5% lower) than the rest of the stocks. In mid-winter (June-July), the large and small size classes of the Kaitaia stock, and the Marlborough Sounds stock underwent large and rapid declines in condition. At the same time the Golden Bay stock exhibited a much smaller decline in condition. These declines in condition were due to spawning (Figure 3.2), and coincided with rapidly declining water temperatures and day lengths (Figure 3.3). Immediately following this decline in condition the Golden Bay and Marlborough Sounds stocks were c. 2% higher condition than the large and small size classes of the Kaitaia stock. Following the mid-winter decline in condition, all of the stocks began to recover and continued to improve condition until the end of the experiment in October.

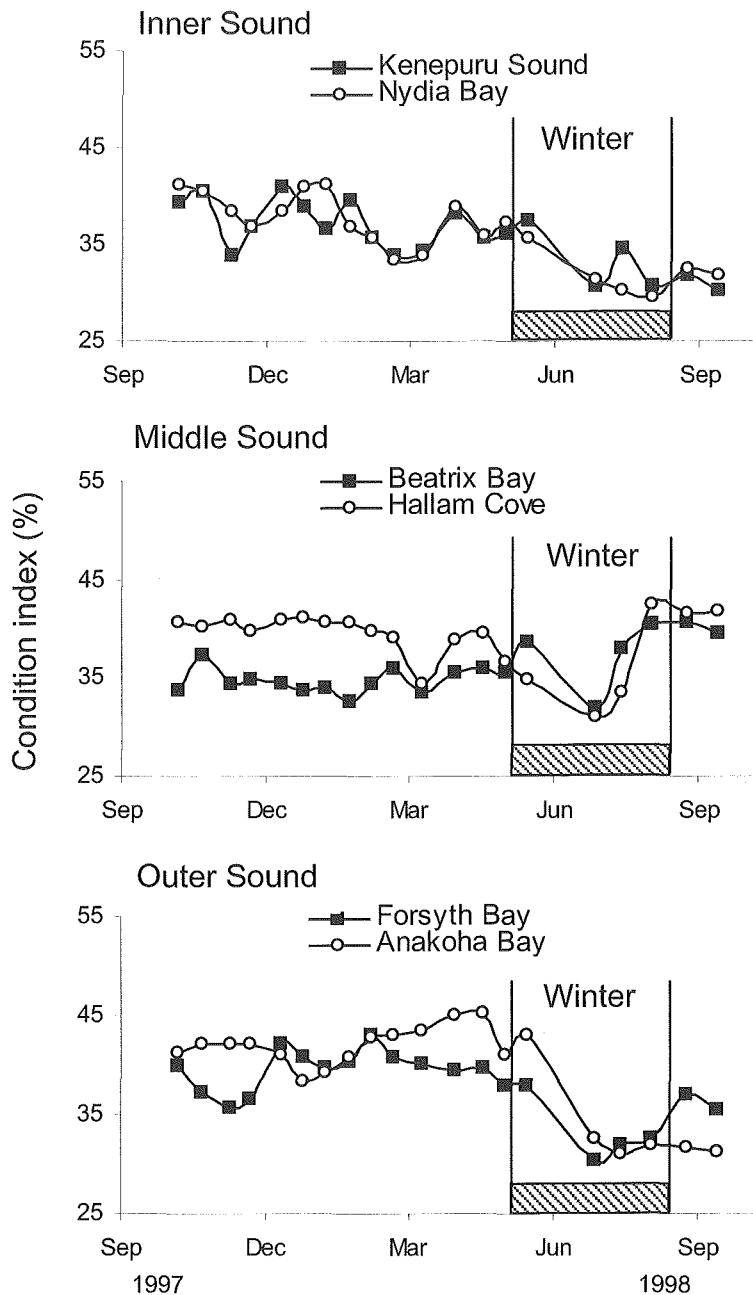


Figure 3.6. Condition cycles of mussels at the three areas (and six sites) in Pelorus Sound between November 1997 and October 1998. Sites are grouped according to the area in Pelorus Sound in which they were located. Confidence intervals have been omitted from the graphs to improve clarity. The mean 95% confidence interval was $\pm 0.6\%$ and values ranged from 0.2 to 1.0%.

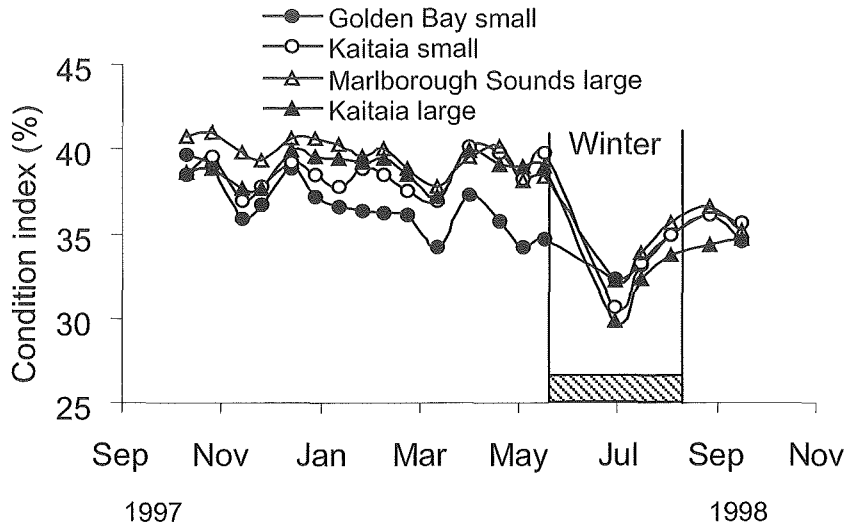


Figure 3.7. Condition cycle of mussel stocks. Each point is the mean condition index for the stock for all six sites ($n = 240$ mussels). Confidence intervals have been omitted from the graphs to improve clarity. The mean 95% confidence interval was $\pm 0.57\%$ and values ranged from 0.39 to 0.89%.

Site (area) \times stock: Site (area) \times stock accounted for $<1\%$ of the variation in condition, but the significance of this term indicated that certain stocks were in better condition than others at some sites (Figure 3.8). The Marlborough Sounds stock was in particularly high condition at Hallam Cove and Kenepuru Sound, and the Golden Bay stock was in particularly poor condition at Kenepuru Sound, Nydia Bay, and Forsyth Bays.

Time \times site (area) \times stock: Time \times site (area) \times stock accounted for 4% of the variation in condition. At certain times and sites some stocks were in significantly higher condition than other stocks. This interaction is reflected in the plots of the differences in condition indices between stocks across spatial and temporal scales (Figure 3.9 & 3.10). The condition of Golden Bay and Marlborough stocks was compared against the Kaitaia stock because the latter is the most common stock used in the mussel industry.

Although there was considerable variation in the condition of mussel stocks across spatial and temporal scales, some patterns were evident. The Marlborough Sounds stock was consistently in greater condition than the Kaitaia stock at Kenepuru Sound and Hallam Cove (Figure 3.9). The Kaitaia stock was generally in higher condition than Golden Bay stock from January 1998 until to June 1998, when the

mussels spawned (Figure 3.10). The higher condition of the Kaitaia stock was particularly evident at Kenepuru Sound and Nydia, Forsyth, and Anakoha Bays. From immediately after the winter decline in condition (June-July) until September, the Golden Bay stock was generally in higher condition than the Kaitaia stock. After September 1998 there was no clear pattern of either stock being consistently in higher condition.

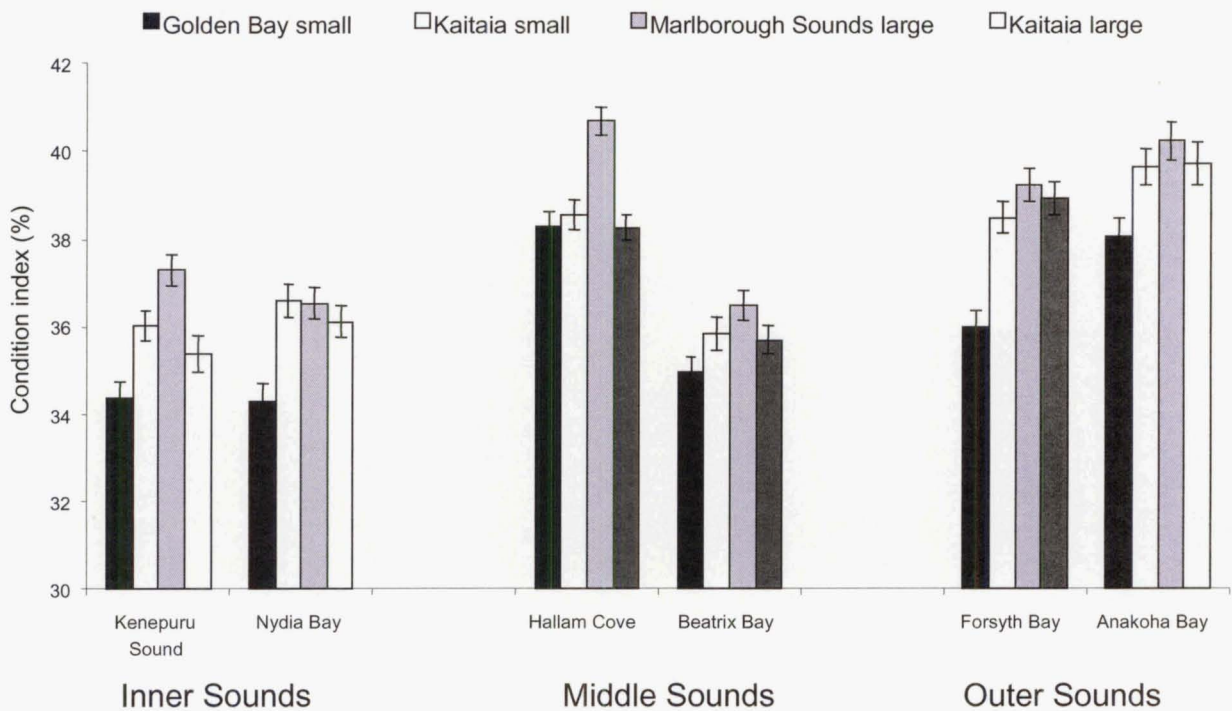


Figure 3.8. Mean condition of Golden Bay, Marlborough Sounds, and Kaitaia stocks at each of the six sites in Pelorus Sound. Mussels were sampled at fortnightly intervals between November 1997 and October 1998. Bars = \pm 95% confidence intervals, $n = 800$ for each treatment.

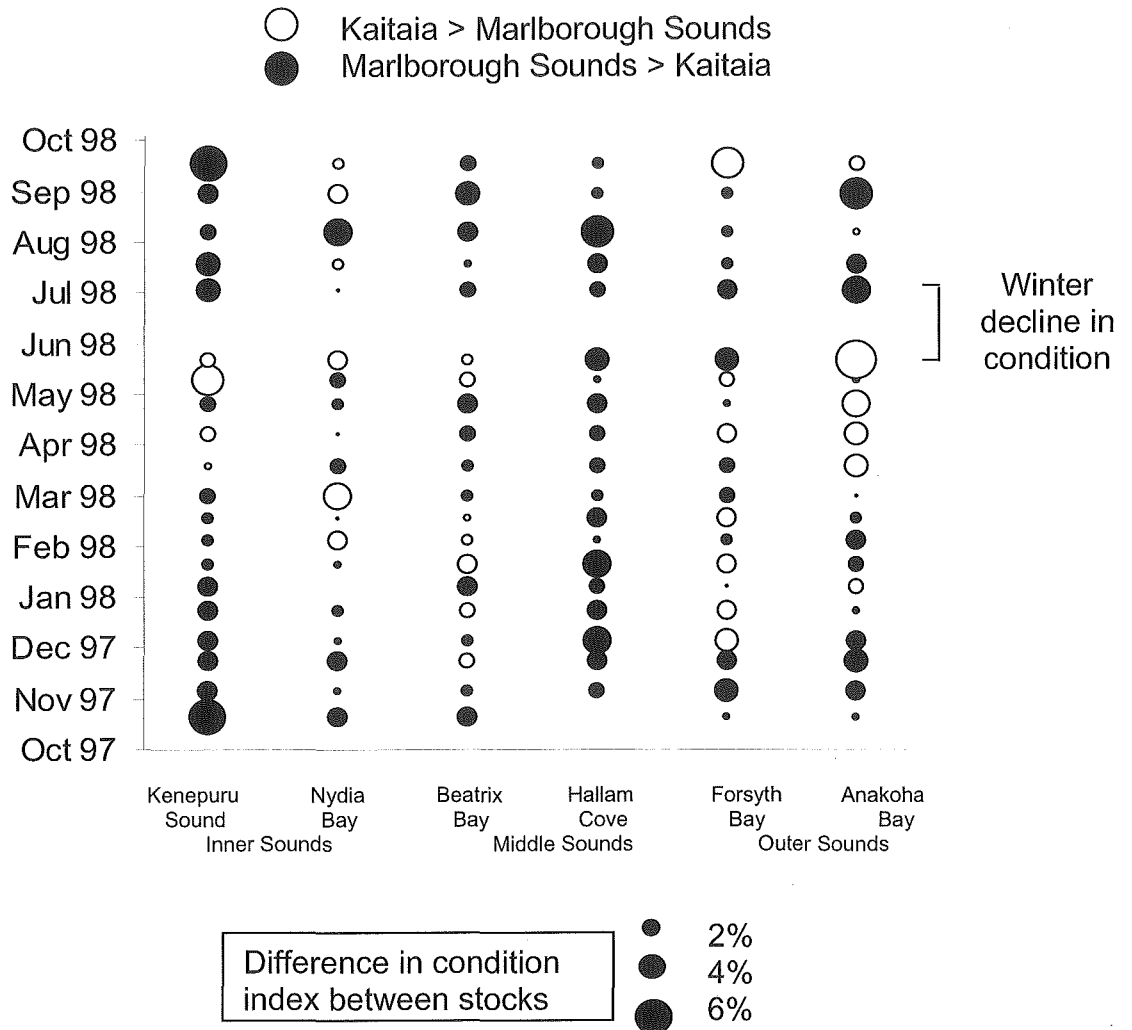


Figure 3.9. Differences in condition between the Marlborough Sounds and Kaitaia stocks. Samples were collected at 120 sites and times. Solid black circles indicate that the Marlborough Sounds (large) stock is in the better condition and white circles indicate that the Kaitaia (large) stock is in the better condition. Sites have been grouped by the area (inner, middle or outer sound) in which they are located. The size of the circle indicates the magnitude of the difference in condition index. The gap in sampling between June and July 1998 was due to mechanical problems with the boat that was used to collect samples.

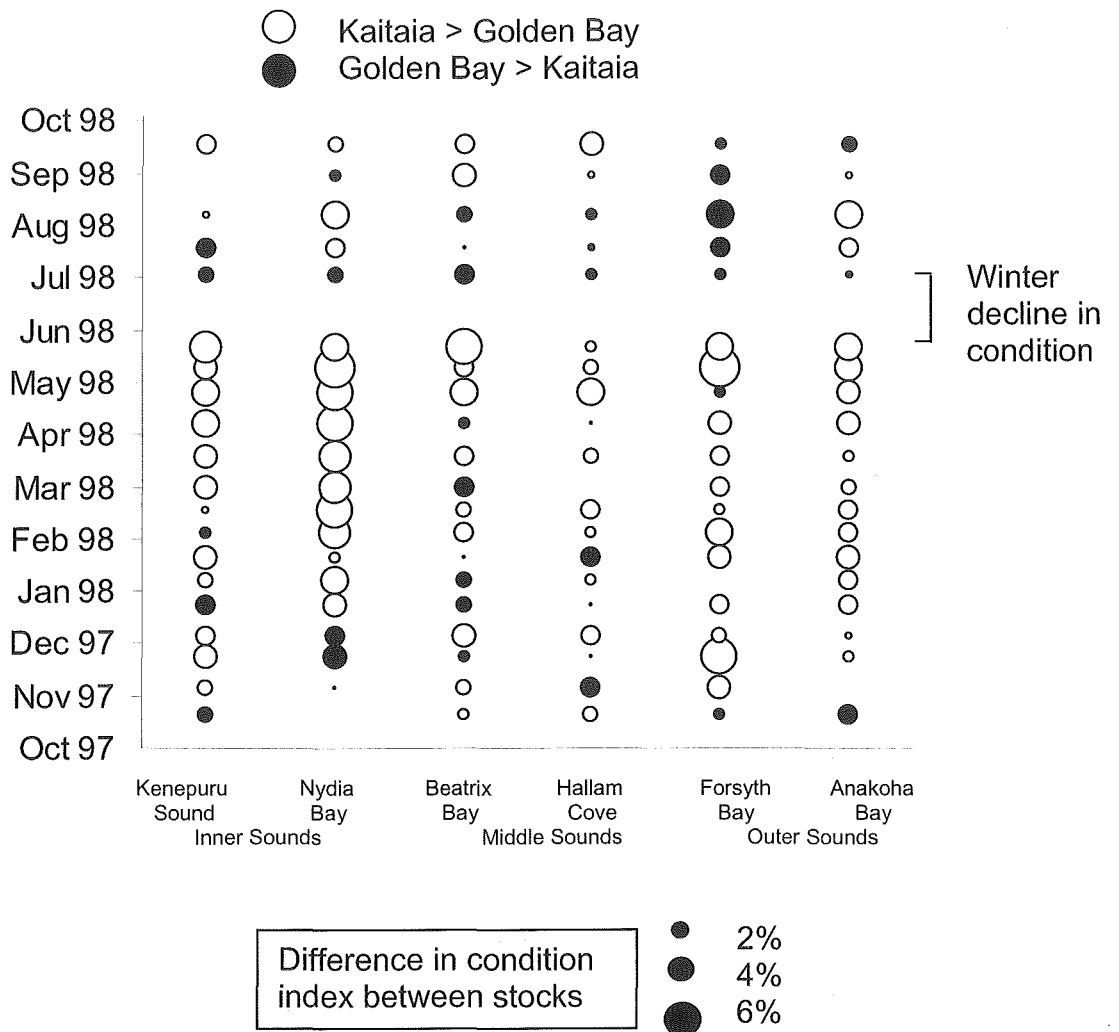


Figure 3.10. Differences in condition between the Golden Bay and Kaitaia stocks. Samples were collected at 120 sites and times. Solid black circles indicate that the Golden Bay (small) stock is in the better condition and white circles indicate that the Kaitaia (small) stock is in the better condition. Sites have been grouped by the area (inner, middle or outer sound) in which they are located. The size of the circle indicates the magnitude of the difference in condition index.

3.3.2 Influence of stock, time, and area on the shell growth rates of mussels

Factors influencing the shell growth of mussels in Pelorus Sound between November 1997 and October 1998 were examined using an analysis of variance (ANOVA). Because the shell growth rate of mussels was constant during the study (Appendix 4), time was not included in the analysis of factors influencing shell growth. To analyse the growth of mussels of different shell lengths in an ANOVA, monthly shell growth rates were calculated (see Appendix 5).

ANOVA – Main effects

Stock: Stock was the only factor that had a significant influence on shell growth of mussels (Table 3.4, Figure 3.11). Although significant, stock accounted for only a small proportion (<1%) of the variation in growth in the model. Golden Bay was the fastest growing stock and grew at 2.3 mm/month; the rest of the stocks grew at 1.8 mm/month. By the end of the experiment the Golden Bay small stock was significantly ($P < 0.01$) longer than the Kaitaia small stock. There was no significant ($P > 0.05$) difference between the Marlborough Sounds large and Kaitaia large stocks (Figure 3.13).

More than 99% of the variation in shell growth of mussels was not explained by the model (i.e., residual SS / total SS = 0.9935).

Table 3.4. ANOVA of factors that may influence the shell growth of mussels. Shell growth rate is the dependent factor and area, site (area), and stock are the independent factors. Area and stock are fixed and site (area) is random and nested within area. The percentage of the variation accounted for by each factor (and interaction) is presented in the % variation column (calculated as the SS for each factor / Σ SS of all factors in model. Asterisk: * = $p < 0.05$).

Factor	DF effect	MS effect	SS	F-value	P-value	% variation
Area	2	57	115	0.9	0.50	0.003
Site	3	66	199	0.4	0.78	0.006
Stock	3	334	1003	4.0	0.04*	0.030
Area × stock	6	22	135	0.3	0.93	0.004
Stock × site (area)	9	83	750	0.4	0.91	0.022
Residual	18216	186	3397316			99.935
Total	18239	751	3399521			100

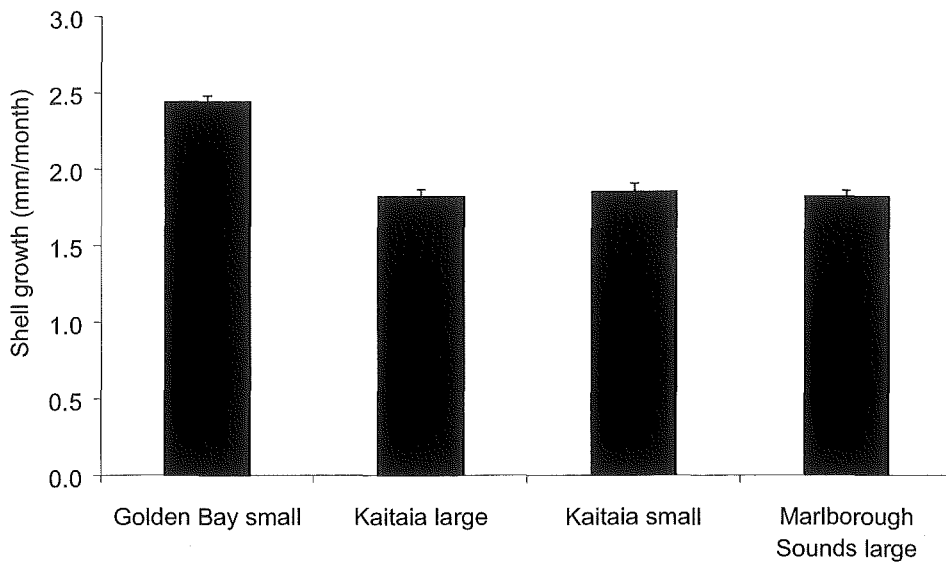


Figure 3.11. Mean shell growth rate of mussel stocks between November 1997 and October 1998. Bars = \pm 95% confidence intervals.

3.3.3 The influence of stock on meat growth

Meat and shell weights determine the condition of mussels (Formula 3.1 Appendix 5). For this reason the change in the meat weight of the mussel stocks was examined (Figure 3.12). The most noticeable feature of the meat growth of the stocks was the difference in growth between the Golden Bay and Kaitaia (small) stocks following winter spawning. Up until the winter spawning event the meat growth of the two stocks was similar, despite the shell growth rate of the Golden Bay stock being higher (Figure 3.13). This resulted in the Golden Bay stock being in poor condition until June 1998 (Figure 3.7). Between June and July both stocks declined in weight. While the Kaitaia stock lost a substantial amount of weight, the Golden Bay stock only slightly decreased in weight. This resulted in the Golden Bay stock being in higher condition than the Kaitaia stock immediately following spawning (Figure 3.7). The meat weight of all the stocks then began to increase. By the end of the experiment the mean meat weight of the Golden Bay stock was 15% higher than the Kaitaia (small) stock.

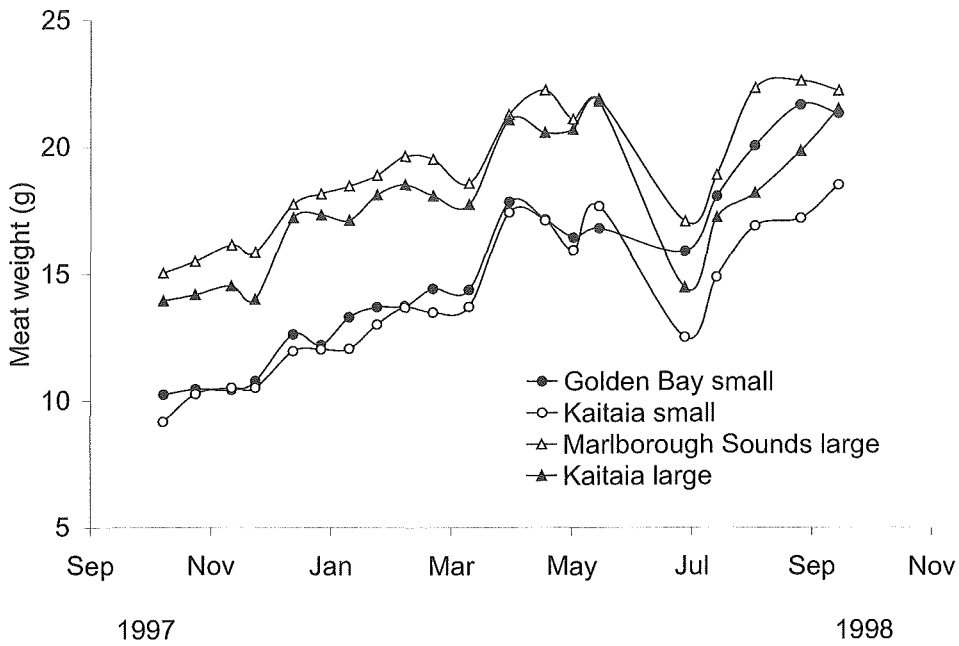


Figure 3.12. Meat weight of mussel stocks between November 1997 and October 1998. Confidence intervals have been omitted from the graphs to improve clarity. The mean 95% confidence interval was ± 0.8 g and values ranged from 0.4 to 1.2 g.

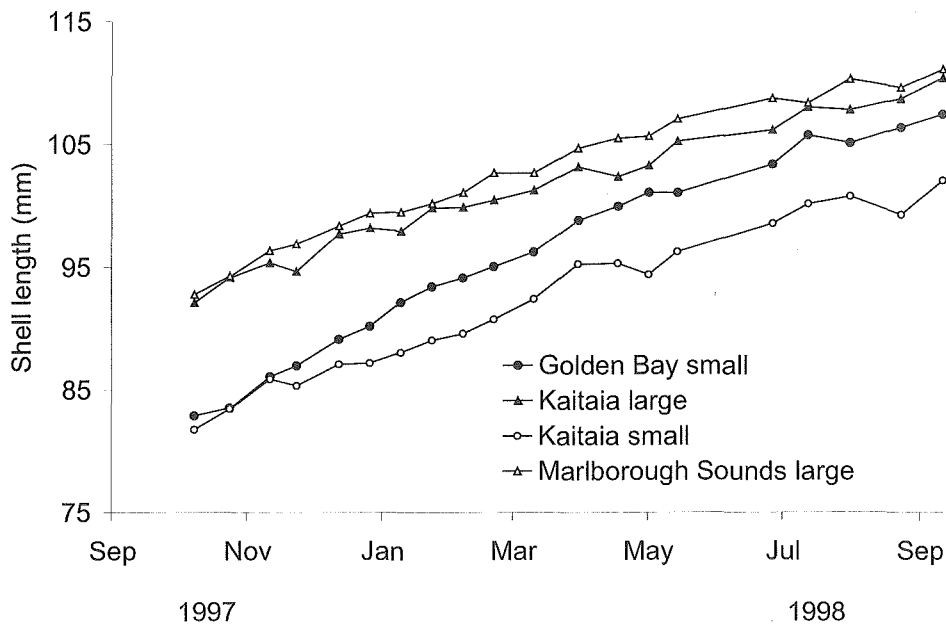


Figure 3.13. Shell growth of Golden Bay, Marlborough, and Kaitaia stocks in Pelorus Sound. Confidence intervals have been omitted from the graphs to improve clarity. The mean 95% confidence interval was ± 0.6 mm and values ranged from 0.4 to 0.8 mm.

3.3.4 Density of droppers at the completion of the experiment

At the completion of the experiment in October 1998, the density of mussels on the experimental droppers was measured. The mean density of the stocks ranged between 75 mussels per metre (Kaitaia small and Marlborough Sounds large) and 84 mussel per metre (Golden Bay small and Kaitaia Large). No significant differences ($p < 0.05$) in density were detected between stocks.

3.4 DISCUSSION

3.4.1 Mid-winter decline in condition

In mid-winter, a large reduction in the condition of mussels was evident at all six study sites. A decline in condition or flesh weight in mid-winter has been documented in several species of bivalves including *Cardium edule* (Hancock 1972), *Mercenaria mercenaria* (Ansell *et al.* 1964), *Tellina tenuis* (Ansell & Trevallion 1967), *Donax vittatus* (Ansell 1972), *M. edulis* (Zwaan & Zandee 1972) and *P. canaliculus* (Hickman *et al.* 1991). These declines are usually attributed to a shortage of food (Ansell & Trevallion 1967, Ansell 1972, Hancock 1972, Kautsky 1982, Loo & Rosenberg 1983) that leads to a “negative energy balance” and the use of stored energy reserves (Gabbott & Bayne 1973). In the present study, however, the concurrent measurement of reproductive state and condition made it clear that the decline in condition was due to spawning.

This is the first study to identify why the condition of farmed *P. canaliculus* in Pelorus Sound is low in winter. The simultaneous decline in condition, to *c.* 30%, throughout Pelorus Sound, also demonstrates why the amount of mussels available to harvest sharply declines at this time (Figure 1.5 Chapter 1).

The existence of a mid-winter (June/July) spawning event is a paradox. The magnitude of the decline in condition suggests that several thousand tonnes of gametes are released. However, no significant spat settlement followed. Even considering that low water temperatures in winter (*c.* 13°C) may extend the normal 3-5 week planktonic stage of mussel larvae (Hayden 1995) by a few weeks (Bourne & Smith 1972), significant spat settlements do not usually occur until November (Hayden & Kendrick 1992, Hayden 1995, New Zealand Marine Farmers and Sealord

Shellfish Ltd. Spat Monitoring Programs). The absence of a winter spat settlement suggests that either the larvae produced by the farmed mussels in Pelorus Sound during winter are non-viable or that the prevailing environmental conditions lead to the mass mortality of larvae.

The simultaneous decline in condition at all six sites indicated that spawning was synchronised, indicating that the spawning stimulus was not site-specific. In winter, spawning coincided with sharply decreasing and near minimum water temperatures and day lengths.

Factors triggering the spawning of commercially important shellfish species have been intensively studied (Chipperfield 1953, Helm & Spenser 1972, Tortell 1980, Utting & Spenser 1991, Thorarinsdottir 1996, Buchanan 1999). Spawning stimuli for oysters and clams held in hatcheries are well understood (e.g. Helm & Spenser 1972, Utting & Spenser 1991): techniques such as heat shock, serotonin injection, exposure to ripe gametes, and agitation are used to induce spawning consistently in mature (gravid) animals. Although these techniques can be effective to stimulate the spawning of *P. canaliculus* (Redfearn 1998, Buchanan 1999), success often varies between studies (e.g. Tortell 1980). This may be due to the difficulties researchers can have obtaining and maintaining mature *P. canaliculus* in hatcheries (S. Buchanan, pers. comm. April 1999).

The search for spawning triggers in wild mussels appears complicated due to the range of stimuli that have been implicated. Strong wave action, lunar cycles, desiccation, salinity changes, changes in day length, and rapidly changing water temperatures have all been suggested as important stimuli (see Bayne 1976 for a review). However, some studies have found spawning to occur with no obvious trigger (Bangli 1978, Tortell 1980) other than the mussels being mature. Considering the broad range of stimuli that have been linked to spawning it appears any of several, even subtle, changes in the environment (such as changing day length or water temperature) can trigger spawning in *P. canaliculus* (and shellfish in general), if they are reproductively mature.

3.4.2 Relationship between mussel condition and chlorophyll *a* levels

There was no correlation between mussel condition and chlorophyll *a* levels. This was notable because phytoplankton is the principal food source of farmed mussels (Shumway *et al.* 1985, Grant 1996, Ross *et al.* 1998a, Gall *et al.* 2000) and chlorophyll *a* is a commonly used proxy for phytoplankton biomass (e.g., Ross *et al.* 1998b). Therefore, it could be expected that a strong relationship should exist between chlorophyll *a* and condition. It could be argued, however, that no studies have demonstrated a definitive link between the two variables (see Grant (1996) for a review). The absence of a relationship between chlorophyll *a* and mussel condition could be due to several factors that are not necessarily mutually exclusive.

First, the collection of chlorophyll *a* samples at intervals of weeks may not adequately quantify the chlorophyll *a*, (and phytoplankton) levels that bivalves are exposed to between samplings. Chlorophyll *a* levels are highly variable spatially and temporally in Pelorus Sound (Gibbs *et al.* 1993, Ogilvie *et al.* 2000). Ogilvie *et al.* (2000) demonstrated this by continuously monitoring chlorophyll *a* levels over four tidal cycles (c. 48 hrs) at a mussel farm in Beatrix Bay. Chlorophyll *a* levels varied by as much as 400% within a single 24 hr period, with values ranging between 1.2 and 5 $\mu\text{g L}^{-1}$. Mean chlorophyll *a* levels also varied between days: in the first 24 hrs of the study values averaged c. 1.8 $\mu\text{g L}^{-1}$ while in the second 24 hrs the mean values rose to c. 2.8 $\mu\text{g L}^{-1}$. Considering this level of variability it would be difficult, or impossible, to quantify the chlorophyll *a* levels accurately that mussels are exposed to without continuous measurements. Hickman *et al.* (1991) also failed to find a correlation between chlorophyll *a* and the condition of farmed mussels in Pelorus Sound. He summarised the situation well by stating “Condition is an integrated measure of feeding, and associated metabolic activities of mussels over a substantial period of time. Environmental data, on the other hand, (often) represents short term or instantaneous measurements, that exhibit different degrees of temporal variability”.

Second, chlorophyll *a* might not be a good proxy for phytoplankton abundance (and mussel food) in all conditions. In Pelorus Sound, the carbon:chlorophyll *a* ratios have been found to vary between 27 and 84 (Mackenzie *et al.* 1986). Changes in both the composition of phytoplankton communities (Burns 1977, Mackenzie *et al.*

1986) and light intensity (Utkilen *et al.* 1983) could alter chlorophyll *a* levels without necessarily influencing the biomass (as measured by carbon levels) of phytoplankton available to mussels.

Third, changes in the condition of mussels are not always a response to the amount of food available. A decline in condition due to spawning at times of high food concentrations (such as during the spring bloom) could also weaken the relationship between condition and chlorophyll *a*.

This study confirms that linking the growth of bivalves to their environment is not simple, and many factors have the potential to disrupt the relationship between condition and chlorophyll *a*. These results do not dispute that phytoplankton abundance is the key determinant of mussel growth, or that chlorophyll *a* is a useful measure of relative phytoplankton abundance in studies where the same parcel of water is sampled multiple times (e.g., Perez-Camacho *et al.* 1991, Ogilvie 2000, Ogilvie *et al.* 2000). Instead, results (from this study and reviews of scientific literature e.g. Grant 1996) suggest complex interactions between physical and biological factors influence mussel condition, and not a single, easily measured variable. This observation is of relevance to the Marlborough Sounds mussel industry, as it highlights the difficulty in measuring mussel food and therefore developing effective models for the sustainability of mussel farming.

3.4.3 The influence of spatial and temporal factors on mussel condition

Spatial and temporal factors were more important than stock in controlling the condition of cultured mussels in Pelorus Sound. For example, at a single sampling time the maximum range in condition index between the six sites was 13% (Figure 3.6), while the maximum range between stocks was 5% (Figure 3.7). The largest range between sites occurred in August 1998 and was a consequence of mussels in the middle sounds recovering quickly from the mid-winter spawning event, while mussels in the outer sounds failed to recover. This highlights that identifying sites where condition has recovered rapidly is important in maximising the condition of harvested mussels following mid-winter spawning. Clearly, the more sites (and areas) that mussel processors have the option to harvest from, the higher the yields they are

likely to achieve. If the processes controlling the large spatial and temporal variations in the condition of farmed mussels could be fully understood and manipulated, increases in mean annual condition index far greater than the 2% discussed in the General Introduction could be achieved.

3.4.4 The influence of stock on mussel condition

Small but statistically significant differences in condition occurred between some mussel stocks. In the seven months leading up to mid-winter spawning the Kaitaia and Marlborough Sounds stocks were in higher condition than the Golden Bay stock. The Kaitaia stock then exhibited the largest decline in condition, of the three stocks during the mid-winter spawning event. As a consequence the mean condition of the Golden Bay and Marlborough Sounds stocks was c. 2% higher than the Kaitaia stock immediately following spawning.

Although several studies have found differences in shell or meat growth between stocks (e.g., Dickie *et al.* 1984, Fuentes *et al.* 1992, Perez-Camacho *et al.* 1995), this is the first study to identify statistically significant differences in the condition cycles of mussel stocks. It is also the first study to identify a time (i.e., the mid-winter spawning event) when the relative condition of stocks changes. The findings are consistent with anecdotal evidence from mussel farmers (Fox 1996) and indicate a small (c. 2 %) increase in condition index might be achieved by selectively harvesting the Marlborough Sounds and Golden Bay stocks immediately following winter spawning (Figure 3.12).

The Marlborough Sounds stock was, on average, in better condition than the rest of the stocks during the study. This fits in with the prediction by Smith (1988) that mussel stocks should grow best in their home environment. If this is typical of spat caught in the Marlborough Sounds, and suitable quantities can be efficiently caught, it would be the obvious stock for the industry to use to maximise the mean condition of harvested mussels.

The differences in condition between mussel stocks seen in this study are of interest as they occurred between stocks exposed to different environments (i.e., mussel farms) before the study. For stock-related traits to be commercially useful,

they need to occur regardless of the environments that the stocks are previously exposed to, as farmed mussels are regularly moved between longlines or farms during the farming cycle.

3.4.5 Influence of stock on shell growth

Stock was the only factor that influenced the shell growth of farmed mussels. The shell growth of the Golden Bay stock was c. 25% higher than the rest of the stocks, at all six sites, over the course of the study. Similarly, the meat growth was c. 15% higher. There are two possible explanations for the differences in growth between stocks and these are not necessarily mutually exclusive. The differences could be due to either environmental or true stock effects (i.e., genetic).

The environment to which mussels are exposed to before being transplanted to a new site has the potential to influence their subsequent growth. Mussels modify their feeding behaviour to maximise energy intake and growth and to compensate for reduced food quantity or quality (Bayne *et al.* 1984 & 1987, Widdows *et al.* 1984, Marsden & Weatherhead 1999). For example, Marsden & Weatherhead (1999) demonstrated that *P. canaliculus* from the mid-intertidal zone compensate for their reduced immersion and feeding times by having higher filtration rates, relative to mussels from the low intertidal zone. Clearance rates in 80 mm mussels from the mid-tidal zone were between 1.3 and 2.9 times greater than mussels from the low-tidal zone. Because Marsden & Weatherhead (1999) carried out their experiment only two days after the mussels were removed from the intertidal zone, it is unclear how long these feeding adaptations persist in *P. canaliculus*. However, in a similar experiment in which two populations of *M. edulis* were reciprocally transplanted to each others home environment, a 40 % difference in clearance rate persisted until the experiment finished six months later (Widdows *et al.* 1984). This type of feeding adaptation could account for the differences in growth in the present study and in all previous studies that have investigated the influence of stock (see Table 1.1). Longer-term experiments are needed to investigate whether the prior growing environment can influence the long term feeding behaviour (and growth) of mussels.

Comparing the results of the present study to those in the next chapter, in which the mussel stocks were exposed to identical conditions from an early age, should indicate whether the differences in growth seen in this study are true stock effects.

Regardless of the process which caused the higher growth in the mussels from Golden Bay, fast-growing mussels would have obvious economic benefits for farmers. For example, by February 1998, when both of the small stocks had reached a size at which mussels are normally harvested (c. 85-90 mm), the mean live weight of the Golden Bay small stock was 12% higher than the Kaitaia small stock (55.6 vs. 49.5 g). If these mussels had been grown using normal farming techniques (180 mussels per metre of rope and 4000 metres of rope per longline), a longline of Golden Bay mussels would have yielded 37.4 tonnes of live mussels and the Kaitaia stock would have yielded 33.3 tonnes. At the current (2002) price of c. \$1200 per tonne the extra 4.1 tonne would have been worth \$4920.

This is the first study to demonstrate quantitatively at a farm-scale that differences in growth may occur between *Perna* spp stocks. These differences in condition and shell growth were detected between stocks which had previously been subjected to normal farming practices, including being exposed to different environments during the spat stage. This is an important observation: if stock-related traits are to be commercially useful, they need to occur regardless of the environments that the stocks have been previously exposed to. However, it is also important to determine whether exposing mussel stocks to different environments influences their subsequent growth potential. Contrasting the results from the present study to those of the next chapter, in which the early growing environment is closely controlled, will provide an insight to whether the early growing environment significantly influences the subsequent growth of mussels. This will determine if the stock-related traits identified in this study are predictable and commercially useful.

Chapter 4

The influence of stock, time, and culture area on the growth of *Perna canaliculus* exposed to a controlled environment during the spat stage

4.1 INTRODUCTION

Several studies have reported that mussel stocks can have different growth rates when grown at the same site (Dickie *et al.* 1984, Mallet & Carver 1989, Kautsky *et al.* 1990, Fuentes *et al.* 1992, 1994, Stirling & Okumus 1994, Perez Camacho *et al.* 1995). For example, Mallet & Carver (1989) reported that during a 14 month study the shell growth rates of nine stocks of *M. galloprovincialis* varied by as much as 19%. A problem with these studies, however, is that the mussel stocks were collected at relatively large sizes (> c. 15 mm). As a consequence they were exposed to different environments for several months prior to the experiments (Dickie *et al.* 1984, Mallet & Carver 1989, Kautsky *et al.* 1990, Fuentes *et al.* 1994, Stirling & Okumus 1994, Perez Camacho *et al.* 1995).

This is an issue because mussels can adapt to their environment and maximise growth by altering their feeding behaviour (Theisen 1977, Widdows *et al.* 1979, Bayne *et al.* 1993, Navarro *et al.* 1995, Marsden & Weatherhead 1999). For example, Marsden & Weatherhead (1999) demonstrated that *P. canaliculus* obtained from the mid-intertidal zone compensated for reduced immersion and feeding times by elevating filtration rates, relative to mussels from the low-intertidal zone. This type of adaptation can persist for at least six months after mussels are moved to a new site (Widdows *et al.* 1984). Therefore, it is possible that the differences in growth between stocks in previous studies were not a result of true stock effects (i.e., with a genetic basis) but rather physiological adaptations to their prior environment (Mallet *et al.* 1987, Perez Camacho *et al.* 1995).

Another issue with previous stock studies is that they were not replicated. It is uncertain whether the same traits (e.g., higher growth rates or different condition cycles) would occur if the experiments were repeated at later date. If traits associated with different mussel stocks are to be commercially exploited, the traits must be a predictable and consistent feature of the stock.

As in Chapter 3, I was particularly interested in determining whether the Golden Bay or Marlborough Sounds stocks are in higher condition than the Kaitaia stock during winter, when farmed mussels are in poor condition (see General Introduction). If the Golden Bay or Marlborough Sounds stocks are in higher condition

over winter, it may be feasible to harvest these stocks instead of the Kaitaia stock. This technique could potentially increase the condition of mussels harvested over winter and minimise many of the problems caused by poor condition (see General Introduction).

This study aims to determine:

1. Whether mussel stocks have different shell growth rates and condition cycles when they are exposed to the same environmental conditions from an early age;
2. Whether the same stock-related traits occur in mussels caught in different seasons;
3. Whether differences in growth between stocks are significant when compared to spatial and temporal factors;

Unlike in Chapter 3, in this series of growth trials the environmental conditions to which the mussel stocks were exposed before the experiments (during the spat stage) were identical. Mussel spat were collected using a new and innovative technique that allowed them to be obtained at the smallest size that is biologically feasible (c. 3.5 mm in length)(see section 4.2.1). Below this size, spat are highly mobile and are capable of migrating off the ropes on which they are seeded (Buchanan 1994). Capturing mussel stocks at a very small size and growing them under identical conditions minimises or eliminates the possibility that any differences in growth or condition are due to the environment that the spat were exposed to before the experiment.

This study uses mussel stocks caught in the summer, autumn, and winter of 1997 to determine whether the same mussel stocks caught at different times exhibit the same traits. Comparing experimental results will provide an insight to whether differences in the early growing environment influences the subsequent growth potential of mussels. The implications of the results are discussed in relation to the current understanding of mussel growth and the potential benefits to the local mussel industry.

4.2 METHODS

4.2.1 Spat catching

Spat catching was attempted at Kaitaia, Golden Bay, and the Marlborough Sounds in the summer, autumn, winter, and spring of 1997. In each season, normal commercial spat catching techniques were used. In Golden Bay and the Marlborough Sounds, spat-catching ropes were hung on mussel farms (Figure 4.1) with a history of successful spat settlement.



Figure 4.1. Spat-catching ropes in Golden Bay.

Spat settlement was monitored at weekly intervals. When the densities of newly settled spat exceeded 5,000 per linear metre of catching rope, spat were washed from the ropes. This was done using a machine developed by Sealord Shellfish Ltd. that used high-pressure jets of water (Figure 4.2 & 4.3). This technique allowed mussel spat to be collected at a much smaller size than in previous studies (see Table 1.1 of the General Introduction). Spat were then sieved through a series of screens of decreasing mesh size to obtain spat between 800 and 3200 μm in shell

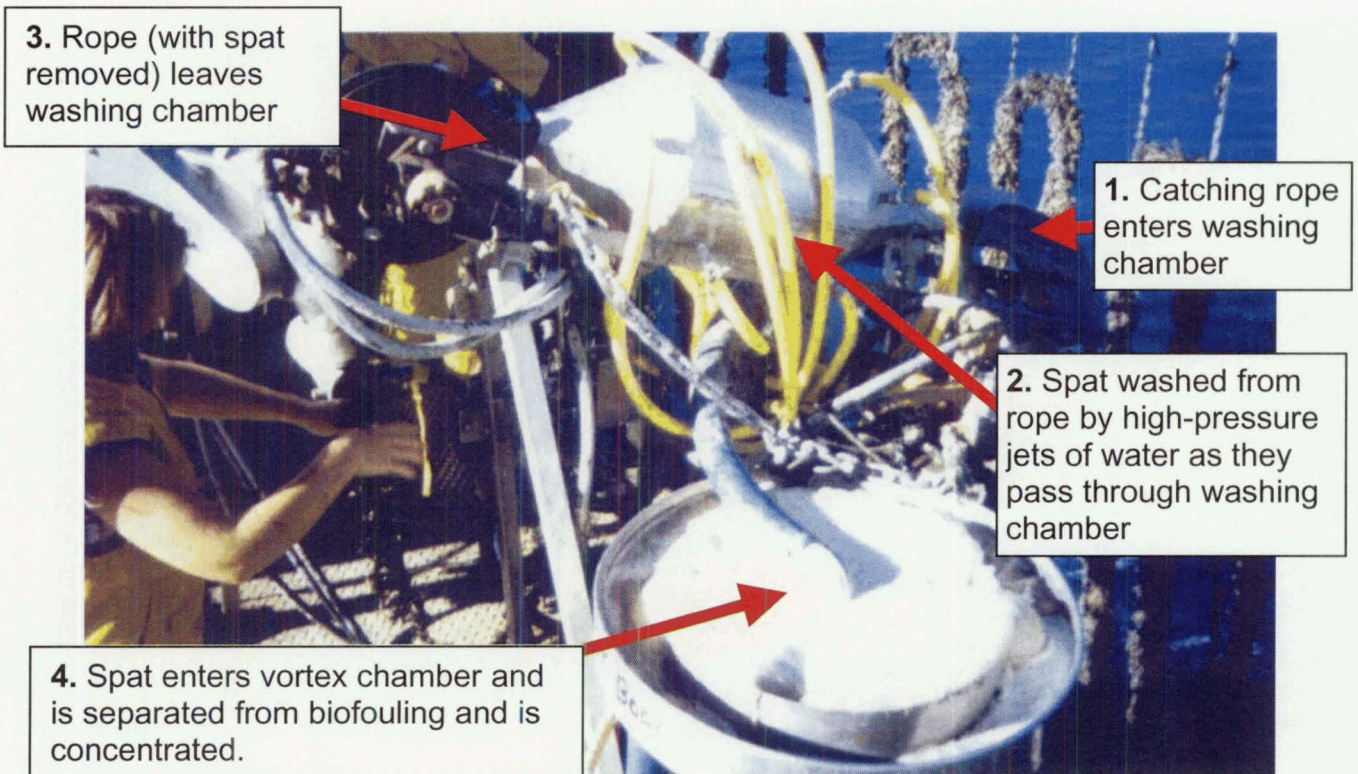


Figure 4.2. Mussel spat being washed from catching ropes. Numbers 1-4 indicate the order in which the spat and rope moves through the spat washing machine.



Figure 4.3 Mussel spat after being washed from the catching ropes and separated from biofouling.

length, which were then used in the growth trials (Figure 4.3). This ensured that all mussel spat were a similar initial size, regardless of where or when they were caught. Standard industry methods were used to obtain Kaitaia spat. Kaitaia spat are washed ashore attached to seaweed on Ninety Mile Beach, near Kaitaia in northern New Zealand (Hickman 1982, 1987). Commercial collectors gathered the spat and trucked it to the Marlborough Sounds. The Golden Bay, Kaitaia, and Marlborough Sounds stocks caught in the summer, autumn, and spring of 1997 were of approximately the same size ($< 3200 \mu\text{m}$ in shell length).

Figure 4.4 is a timeline that schematically displays how mussel spat were managed between January 1997 and October 1999. It includes the seasons in which successful spat catches were made, the stocks that were caught, the dates when spat were seeded onto ropes, and when the sampling of mussels began. In the summer and autumn of 1997 mussel spat were caught at Golden Bay, Kaitaia, and the Marlborough Sounds. No successful spat catches were made in the winter of 1997. In the spring of 1997 successful spat catches were only made in Golden Bay and Kaitaia.

4.2.2 Ongrowing spat in Hallam Cove

Hallam Cove was selected as a site to on-grow the mussel spat (see Figure 2.2 in Chapter 2 for the location). The site was chosen due to its proximity to the Sealord Laboratory in Elaine Bay and because it was sheltered. A summary of the physical and biological characteristics of the site is given in Table 2.1 in the General Methods. Hallam Cove is a relatively deep site (25m) with clear water and slow currents ($< 20 \text{ cm s}^{-1}$) and it is not strongly influenced by freshwater from the Pelorus River (mean salinity = 31.2 ppt).

Each treatment (a stock caught within a season) was seeded onto ropes at a density of c. 4,000 spat per linear metre of rope. As a part of the normal seeding process, freshly seeded spat were held in place with mussel stocking. This was done

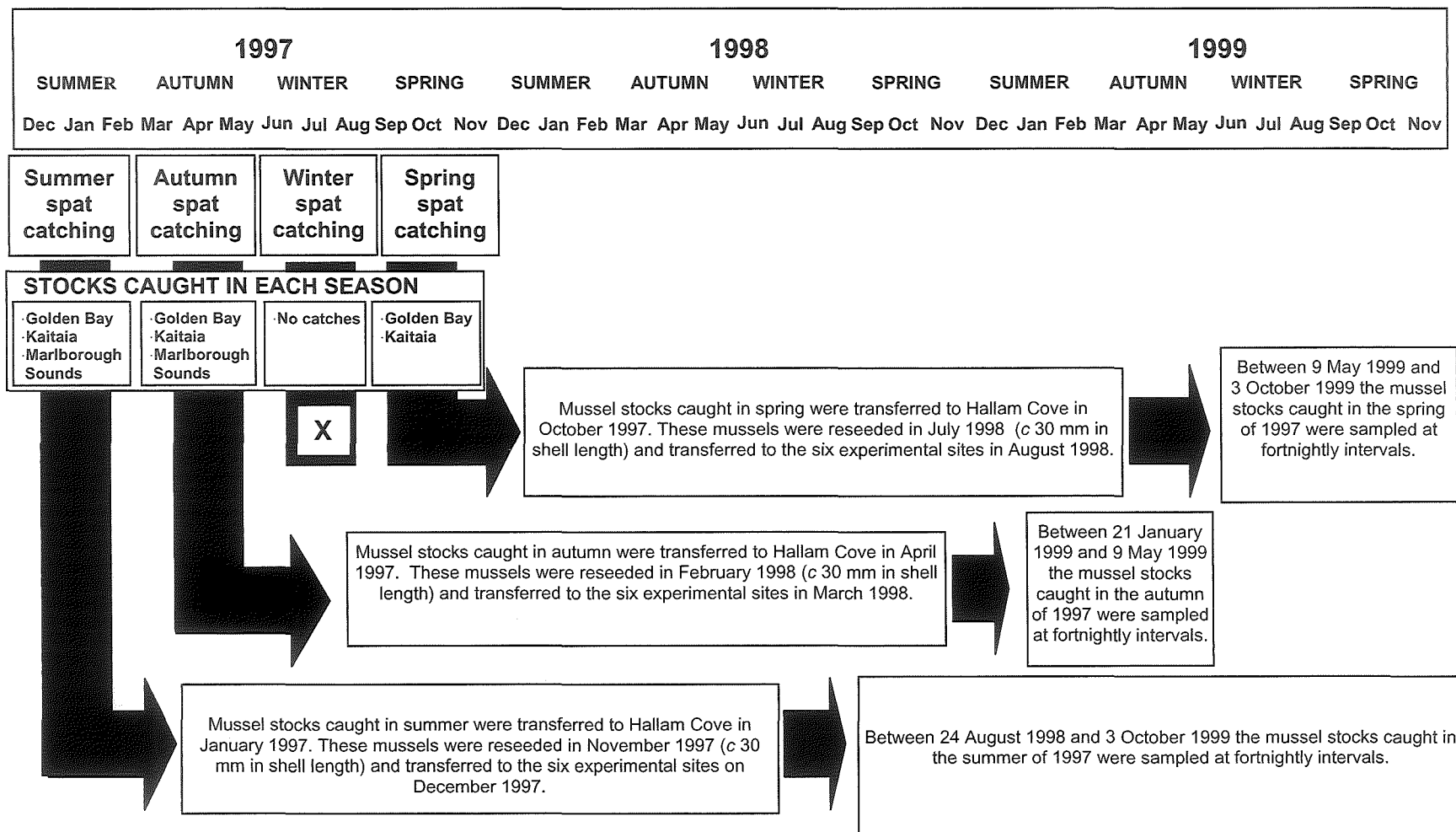


Figure 4.4 Timeline of the capture, reseeded, and sampling of mussels. Once the mussels reached c. 30 millimetres in length they were reseeded at 170 mussels per metre of rope. One month after reseeded, two 5-metre droppers of each stock were transferred to each of the six experimental sites. A full description of the experimental design and sampling protocols are outlined in Figure 4.5a-c and section 4.2.4 of the methods section.

to increase the number of spat that attach to the rope. In each of the successful spat-catching seasons the stocks were seeded onto ropes within two weeks of each other. Stocks caught in each of the seasons were hung in randomised positions along a single longline in Hallam Cove.

Mussels caught in summer, autumn, and spring were held in Hallam Cove until they reached c. 30 millimetres in shell length. Each of the treatments was seeded onto a length of rope at a density of 170 mussels per metre. Following final seeding, the mussels were held in Hallam Cove for a further month to allow new byssal threads to develop fully. Then each treatment was cut into 5 m experimental droppers. Two replicate droppers of each treatment were then transferred to the six study sites (see Figure 4.4 for dates). The mussels were grown at each site until they reached c. 80 mm in shell length, after which sampling began.

4.2.3 Oversettlement

The natural oversettlement of wild spat onto the Kaitaia, Golden Bay, and Marlborough Sounds spat held in Hallam Cove had the potential to confound the experiment. Therefore, oversettlement was estimated using blank 50-centimetre lengths of spat catching rope that were hung at 1-, 5-, and 10-metre depths at each end and the middle of the longline in Hallam Cove. At 2-monthly intervals, one 50-centimetre length of spat catching rope from each of the three positions along the longline was collected, and the newly settled spat were counted. This procedure continued until all of the treatments were transferred to the six experimental sites. The cumulative oversettlement of wild spat did not exceed 5% of the total number of spat present from the planned seeding events. This indicates oversettlement was insufficient to compromise the experiment.

Detailed descriptions of the study sites, protocols used to collect water and mussel samples, and the data storage and analysis techniques are described in the General Methods (section 2.2 - 2.5 of Chapter 2). The calculation of the monthly shell growth rates of mussels, so that shell growth could be analysed in an ANOVA model, is given in Formula 3.1 in Chapter 3.

4.2.4 Growth trials

Factors influencing the condition and growth of *P. canaliculus* were examined in three growth trials. The trials included mussels caught in a) the summer of 1997 which were sampled between August 1998 and October 1999 (Trial 1) b) the autumn of 1997 which were sampled between January 1999 and May 1999 (Trial 2) and c) the spring of 1997 which were sampled between May 1999 and October 1999 (Trial 3). The sampling of mussels in the growth trials overlapped, but the large sample sizes precluded the concurrent sampling of mussels in more than two trials. Therefore, mussels in Trial 1 and 2 were concurrently sampled between January and May 1999. Between May 1999 and October 1999 mussels in Trial 1 and 3 were concurrently sampled. Comparisons of the growth and density of mussels in different trials were only made during the periods they were concurrently sampled.

Each trial was analysed separately, allowing a robust analysis to be made with a balanced ANOVA model. The first growth trial was the largest and included growth data on 14,440 mussels. It was unique as it provided information on the growth of three mussel stocks in three areas and two sites (within each area) at fortnightly intervals over a long period (13 months) (Figure 4.5a). The second and third trials were smaller, spanning four and six months, and provided growth data on 4320 and 3840 mussels respectively. Time, stock, area, and site were included as factors in the ANOVAs that were used to analyse shell growth and condition of mussels in the three growth trials (Figure 4.5a - c).

The protocol used to collect mussels in each trial was identical. At approximately fortnightly intervals, 20 mussels were collected from each duplicate dropper of each stock, at the two sites in each of the three areas of Pelorus Sound (see textured areas on Figures 4.5a - c).

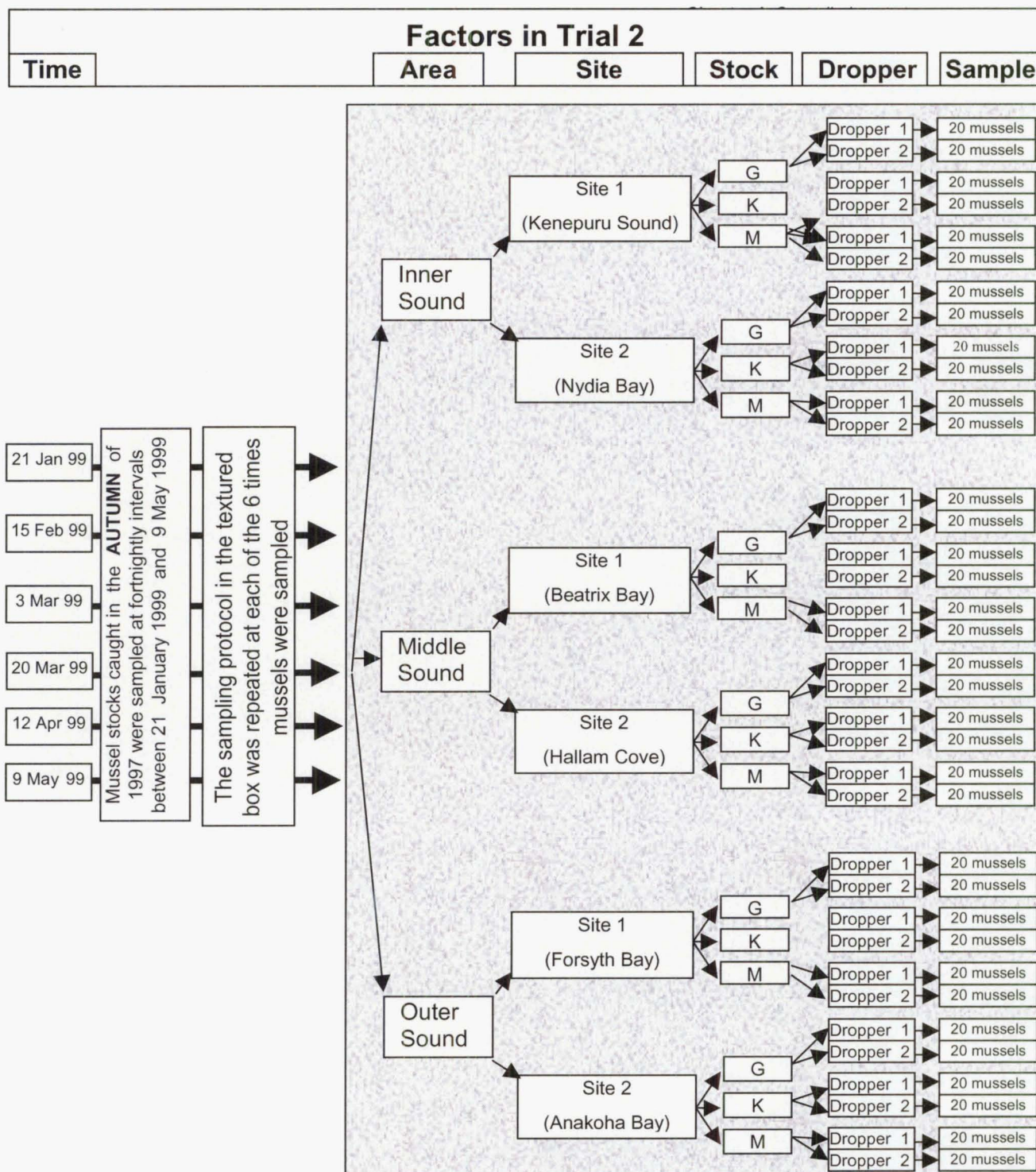


Figure 4.5b Hierarchical model of the experimental design used in Trial 2. Each fortnight 20 mussels were collected from each replicate dropper of each stock (G, M, or K), at each site in each area. G = Golden Bay stock, K = Kaitia stock and M = Marlborough Sounds stock. Mussel stocks caught in Trial 1 and 2 were concurrently sampled between 21 January 1999 and 3 October 1999.

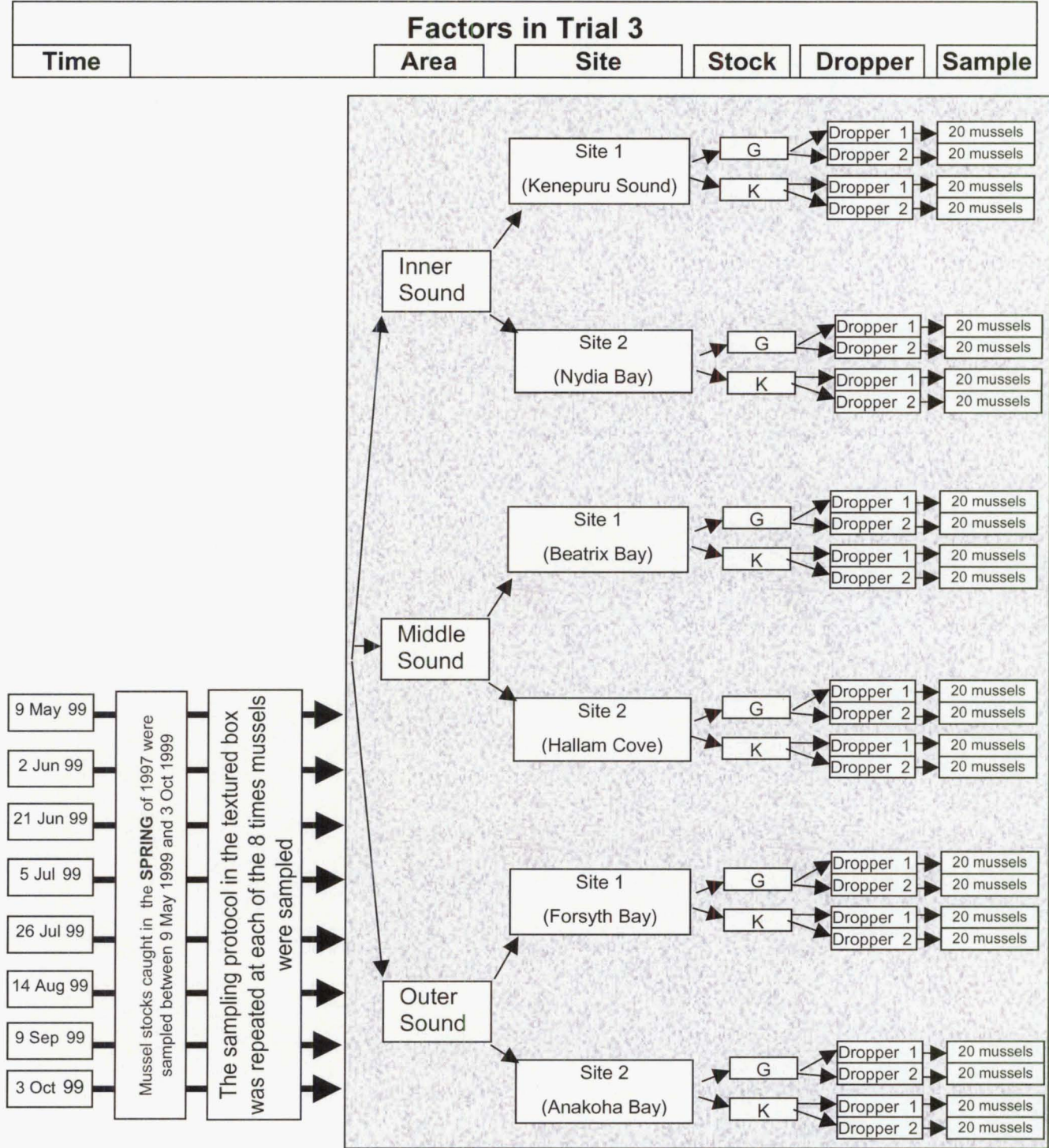


Figure 4.5c Hierarchical model of the experimental design used in Trial 3. Each fortnight 20 mussels were collected from each duplicate dropper of each stock (G or K), at each site in each area. G = Golden Bay stock and K = Kaitaia stock. No Marlborough Sounds stock was caught in spring, therefore this comparison was included in the analysis. Mussel in Trial 1 and 3 were concurrently sampled 9 May 1999 and 3 October 1999.

4.3 RESULTS

Factors influencing the shell growth rate and condition of mussels in Trial 1, 2, and 3 were examined using three ANOVAs. Only the significant factors directly related to the aims of this chapter are discussed in detail and presented graphically. This includes factors that explained a large proportion of the variation in shell growth or condition, and factors that provided evidence as to whether the same stock related traits occurred in each of the three trials. The significant factors (and interactions) are addressed in the hierarchical order in which they are examined in the ANOVA models.

4.3.1 Influence of stock, time, and area on the shell growth rates of mussels

As in Chapter 3, the shell growth rate of mussels within each of the three trials was constant through time (Appendix 7). Time was, therefore, excluded as a factor in the ANOVA of shell growth rate. There was no significant dropper effect ($p > 0.25$) for either the shell growth or condition data, so data from replicate droppers were pooled. To analyse the growth of mussels with different shell lengths (Appendix 8, Figure 4) in an ANOVA, monthly shell growth rates were calculated (see Appendix 5). As in Chapter 3, most the variation in shell growth ($>97\%$) was not explained by the ANOVA models.

ANOVA - Main effects Trial 1

Site (area): Site (area) was the only factor that significantly influenced the shell growth rate of mussels (Table 4.1a). Growth rates were highest at Hallam Cove (1.1 mm/month) and the lowest in Beatrix Bay (0.65 mm/month) (Figure 4.6).

ANOVA - Main effects Trial 2 & 3

Area: Area was the only factor that had a significant effect on shell growth rate in Trial 2 (Table 4.1b).

Site (area): Site (area) was the only factor that significantly influenced the shell growth of mussels in Trial 3 (Table 4.1c).

Table 4.1. ANOVAs of shell growth data of mussels in Trial 1, 2, and 3. Data were collected between August 1998 and October 1999 in Trial 1, between January 1999 and May 1999 in Trial 2, and between May 1999 and October 1999 in Trial 3. Shell growth rate (mm/month) is the dependent factor and area, site (area), and stock are the independent factors. Area and stock are fixed factors and site (area) is a random factor. Site is nested within area. The percentage of the variation accounted for by each factor (and interaction) is presented in the % variation column (calculated as the SS for each factor / Σ SS of all factors in model). Asterisks: *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$.

a) Trial 1

Factor	DF effect	MS effect	SS	F	P-value	% variation
Area	2	61	122	0.57	0.62	0.032
Site (area)	3	108	324	3.83	0.01**	0.084
Stock	2	3	6	0.26	0.78	0.002
Area \times stock	4	10	41	0.95	0.50	0.011
Stock \times site (area)	6	11	66	0.39	0.89	0.017
Residual	13662	28.2	385268			99.855
Total	13679		385827			100.000

b) Trial 2

Factor	DF Effect	MS Effect	SS	F	P-value	% variation
Area	2	539	1077	9.62	0.04*	0.024
Site (area)	3	56	168	0.46	0.71	0.034
Stock	2	2	4	0.02	0.98	0.001
Area \times stock	4	23	93	0.19	0.94	0.021
Stock \times site (area)	6	123	735	1.00	0.42	0.016
Residual	3582	123	440586			99.531
Total	3599		442663			100.000

c) Trial 3

Factor	DF Effect	MS Effect	SS	F	P-value	% variation
Area	2	1693	3387	1.39	0.37	0.554
Site (area)	3	1217	3651	6.82	0.00***	0.597
Stock	1	2155	2155	1.36	0.33	0.533
Area \times stock	2	1232	2463	0.77	0.54	0.403
Stock \times site (area)	3	1210	3630	1.34	0.45	0.594
Residual	3348	178	595944			97.499
Total	3359		611230			100.000

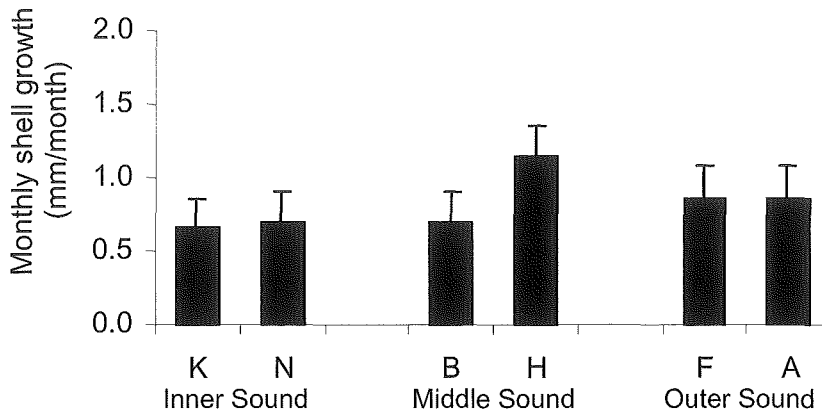


Figure 4.6. Mean monthly shell growth rate of mussels in Trial 1. K = Kenepuru Sound, N = Nydia Bay, B = Beatrix Bay, H = Hallam Cove, F = Forsyth Bay and A = Anakoha Bay. Sites have been grouped by area. Bars = \pm 95% confidence intervals.

4.3.2 Influence of stock, time, and area on the condition of mussels

The factors influencing the condition of mussels in Trial 1, 2, and 3 in Pelorus Sound between August 1998 and October 1999 were examined using ANOVAs (Table 4.2a-c). In this section, the factors that had a significant influence on the condition of mussels in each of the three trials are discussed. The significant factors are highlighted with asterisks in Table 4.2. The factors (and interactions) examined in Trial 1, 2, and 3 accounted for 58%, 34%, and 50% of the total variation in condition respectively. The remaining (residual) variation was not explained for by the factors in the model.

It is noted that the highest order interactions (e.g. Time \times site (area) \times stock) in all three ANOVA models (trials 1-3) were significant and that significant single factors (e.g. Time) would contribute unequally to these higher order interactions.

ANOVA - Main effects Trial 1

Time: Time accounted for 30% of the variation in condition. Condition was generally high between August 1998 and June 1999 but did decrease from c. 40% to 35% over the period. During June and July condition sharply declined from 35% to 30% (Figure 4.7). From July until the end of the study condition remained low. As was seen in the experiment in Chapter 3 the decline in condition during June and July coincided with a shift from most mussels (>90%) being mature to all of the mussels

being less mature. This indicated that a significant spawning event caused the decline in condition. Condition was correlated with both day length and water temperature (Table 4.3), but not salinity or chlorophyll *a*.

Table 4.2. ANOVAs of condition data of mussels in Trial 1, 2, and 3. Data were collected between August 1998 and October 1999 in Trial 1, between January 1999 and May 1999 in Trial 2, and between May 1999 and October 1999 in Trial 3. Condition is the dependent factor and time, area, site (area), and stock are independent factors. Time, area, and stock are fixed factors and site (area) is a random factor. Site is nested within area. The percentage of the variation accounted for by each factor (and interaction) is presented in the % variation column (calculated as the SS for each factor / Σ SS of all factors in model). Asterisks: *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$.

a) Trial 1

Factor	DF effect	MS effect	SS	F-value	P-value	% variation
Time	19	7851	149177	22	0.00***	29.5
Area	2	5044	10088	2	0.24	1.9
Site (area)	3	2121	6364	137	0.00***	1.2
Stock	2	154	308	2	0.26	0.1
Time \times area	38	2473	93968	7	0.00***	17.9
Time \times site (area)	57	353	20096	23	0.00***	3.8
Time \times stock	38	186	7087	2	0.00*	1.3
Area \times stock	4	222	890	2	0.16	0.2
Site (area) \times stock	6	93	557	6	0.00***	0.1
Time \times area \times stock	76	97	7400	1	0.33	1.1
Time \times site (area) \times stock	114	89	10180	6	0.00***	1.9
Residual	14046	15	217123			41.9
Total			523237			100.0

b) Trial 2

Factor	DF effect	MS effect	SS	F-value	P-value	% variation
Time	5	1299	6358	4.53	0.01***	6.5
Area	2	2727	5453	2.14	0.26	5.6
Site (area)	3	1274	3822	84.26	0.00***	3.9
Stock	2	1438	2876	16.81	0.00***	2.9
Time \times area	10	120	1198	0.42	0.92	1.2
Time \times site (area)	15	287	4306	18.98	0.00***	4.4
Time \times stock	10	218	2179	1.59	0.16	2.2
Area \times stock	4	125	500	1.46	0.32	0.5
Site (area) \times stock	6	86	513	5.66	0.00***	0.5
Time \times area \times stock	20	101	2017	0.74	0.76	2.0
Time \times site (area) \times stock	30	137	4106	9.05	0.00***	4.2
Residual	4212	15	63690			65.5
Total	4319		97156			100

c) Trial 3

Factor	DF effect	MS effect	SS	F-value	P-value	% variation
Time	7	1424	9968	2.48	0.04*	8.8
Area	2	232	464	0.35	0.73	0.4
Site (area)	3	670	2010	26.58	0.00***	1.8
Stock	1	3460	3460	7.67	0.07	3.1
Time × area	14	462	6470	0.80	0.66	5.7
Time × site (area)	21	575	12069	22.80	0.00***	10.7
Time × stock	7	706	4940	2.44	0.04*	4.4
Area × stock	2	230	459	0.51	0.65	0.4
Site (area) × stock	3	451	1353	17.90	0.00***	1.2
Time × area × stock	14	662	9272	2.0	0.05	8.2
Time × site (area) × stock	21	289	6072	11.47	0.00**	5.4
Residual	3744	25	56538			50.0
Total	3839		113075			100.0

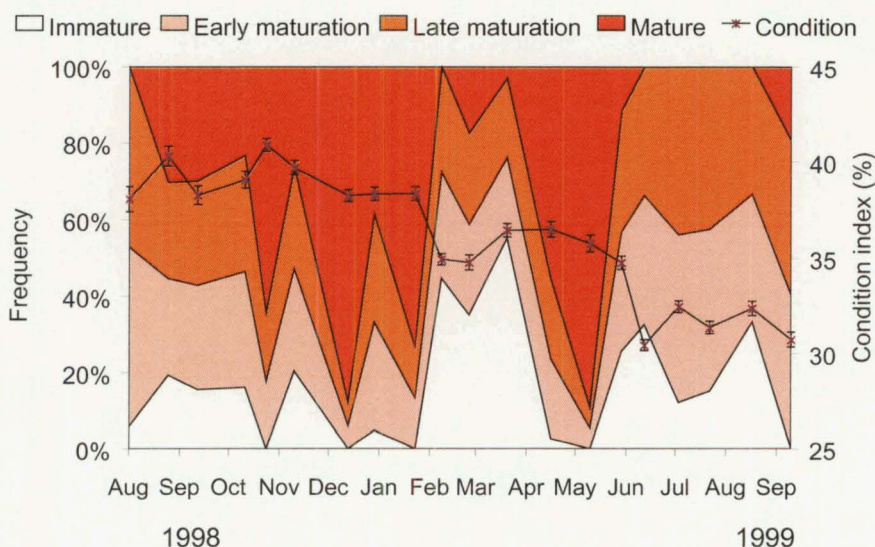


Figure 4.7. Changes in condition index and reproductive state of all mussels sampled between August 1998 and September 1999. Full descriptions of each reproductive stage are given in table 2.1b of the General Methods. Data were grouped for all six sites. Bars = \pm 95% confidence intervals for condition indices ($n=22,560$).

Table 4.3. Spearman's Rank Correlation coefficients (r -values) between mussel condition and water temperature, day length, salinity, and chlorophyll a . Significant relationships are in bold ($n=20$).

	Temperature ($^{\circ}\text{C}$)	Day length (hrs)	Salinity (ppt)	Chlorophyll a ($\mu\text{g/L}^{-1}$)
Condition	0.53 ($p=0.01$)	0.82 ($p=0.01$)	0.04 ($p=0.54$)	0.04 ($p=0.34$)

Site (area): Site (area) accounted for 1% of the variation in condition. The largest difference in the mean condition between sites within an area was 3% and occurred in the outer sound (Figure 4.8). Sites located in the inner and middle sound had similar mean condition indices.

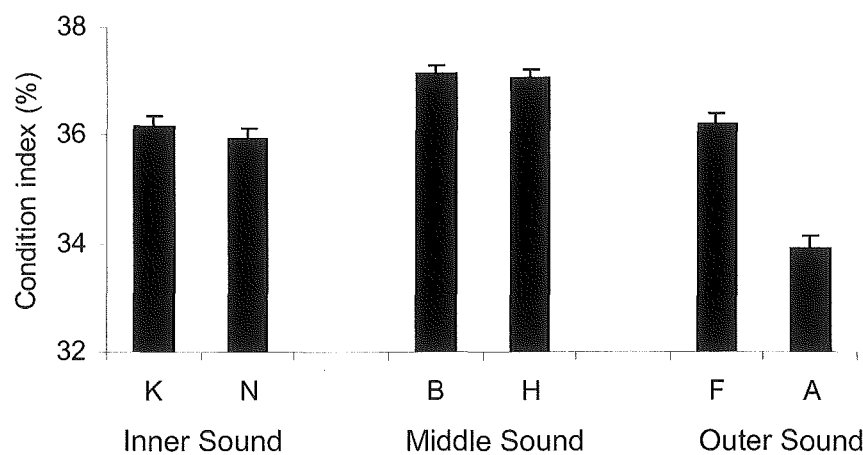


Figure 4.8. Mean condition index of mussels at each study site during Trial 1. K = Kenepuru Sound, N = Nydia Bay, B = Beatrix Bay, H = Hallam Cove, F = Forsyth Bay, A = Anakoha Bay. Sites have been grouped according to the area in Pelorus Sound in which they were located. Bars = \pm 95% confidence intervals.

ANOVA - Interactions Trial 1

Time \times area: Time \times area accounted for 18% of the variation in condition and indicated that the condition cycles of mussels varied between the three areas of Pelorus Sound. The condition cycle of mussels in the middle sound was particularly distinctive: between August 1998 and March 1999 condition declined from c. 50% to c. 35% (Figure 4.9). In contrast, the condition of mussels in the inner and outer sounds started off in about 35% in August 1998 and did not decline over the same period.

Time \times site (area): Time \times site (area) accounted for 4% of the variation in condition. This interaction demonstrated that, at times, there were significant differences in condition cycles between sites (Figure 4.9). These differences were evident following the mid-winter decline in condition in the middle and outer sounds. In the middle Sounds, mussels in Beatrix Bay were generally in higher

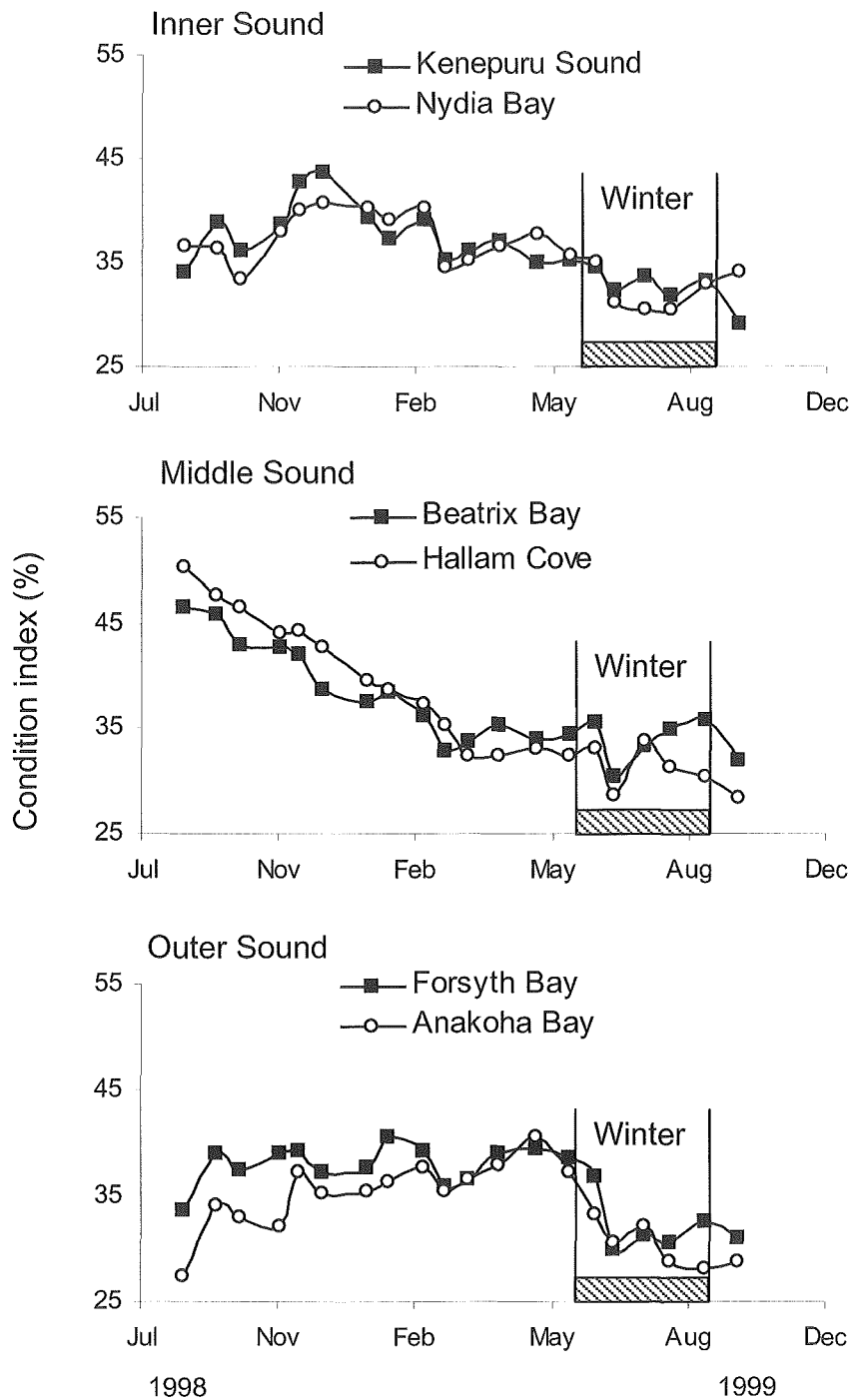


Figure 4.9. Condition indices of mussels during Trial 1. Sites are grouped according to area in Pelorus Sound in which they were located. Each point is the mean of 120 mussels. Confidence intervals have been omitted from the graphs to improve clarity. The mean 95% confidence interval was $\pm 0.6\%$ and values ranged from 0.2 to 1.0%.

condition than mussels in Hallam Cove. In the outer sound, mussels at Forsyth Bay were generally in better condition than mussels grown in Anakoha Bay.

Time × stock: Time × stock accounted for <1% of the variation in condition. This interaction was of interest as it indicated that the condition cycles of the stocks were statistically different (aim one of the study) (Figure 4.10a). The condition indices of the three mussel stocks were similar from August 1998 until March 1999. However, between March and June 1999 the Golden Bay stock tended to be in slightly lower condition (up to 2.5% lower) than the rest of the stocks. Between June and July all three stocks declined in condition. After this mid-winter decline in condition and until the end of the experiment the Golden Bay stock was in higher (c. 2%) condition than the Kaitaia stock. Over the same period the condition of the Marlborough Sounds stock fluctuated between that of the Kaitaia and Golden Bay stocks. Ninety-five percent confidence intervals (see figure 4.10 caption) indicate that differences in condition indices between stocks greater than c. 1.2% were statistically significant.

Site (area) × stock: Site (area) × stock explained <1% of the variation in condition. This interaction indicated that certain stocks were in better condition than others at some sites (Figure 4.11). The Golden Bay stock was in particularly high condition at Nydia Bay.

Time × site (area) × stock: Time × site (area) × stock explained 2% of the variation in condition and is discussed in conjunction with the results from Trial 2 and 3.

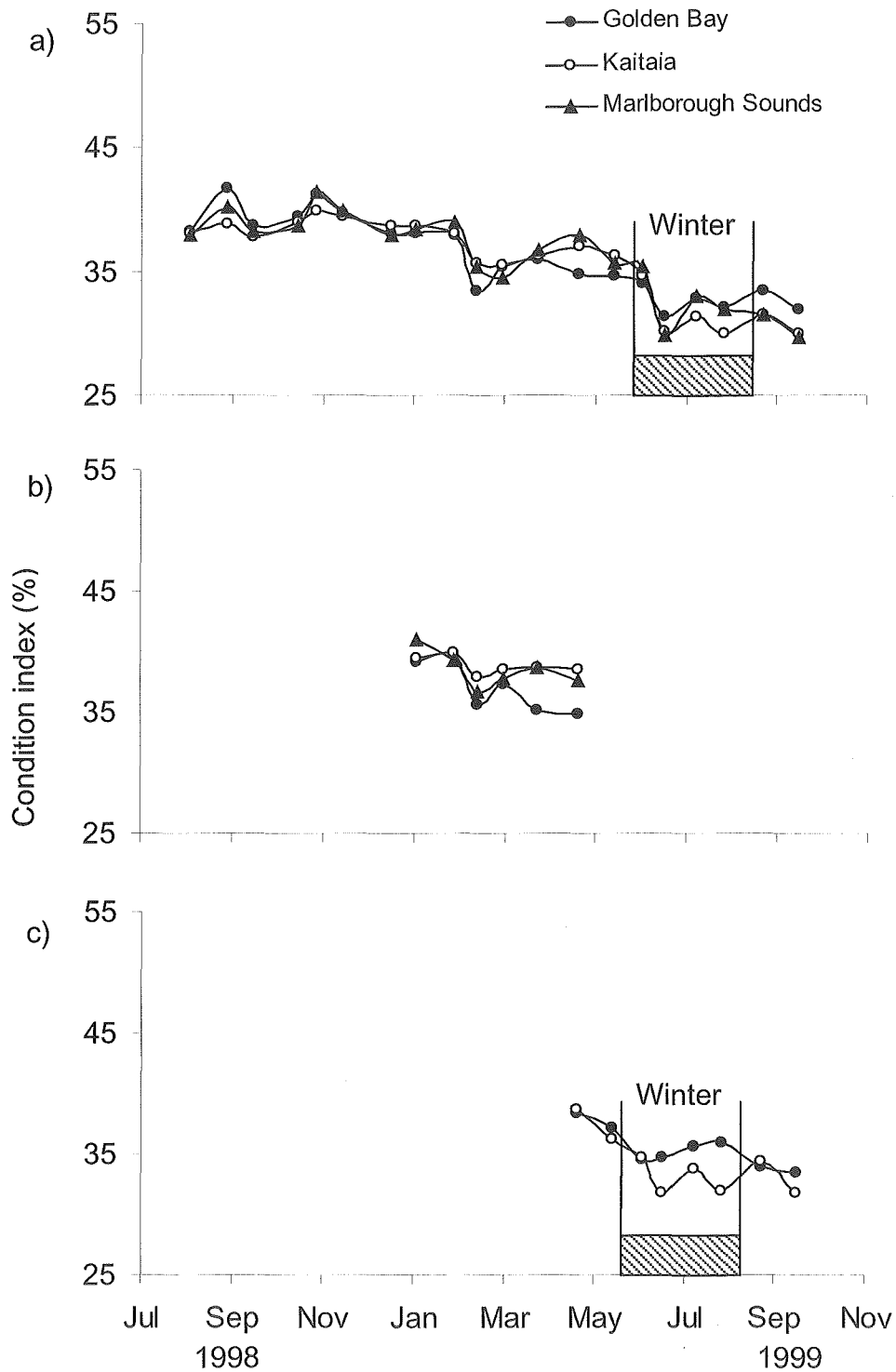


Figure 4.10. Condition indices of mussels in a) Trial 1, b) Trial 2, and c) Trial 3. Each point is the mean condition index for the stock for all six sites ($n = 240$ mussels). Confidence intervals have been omitted from the graphs to improve clarity. The mean 95% confidence interval was $\pm 0.60\%$ and values ranged from 0.41 to 0.91%.

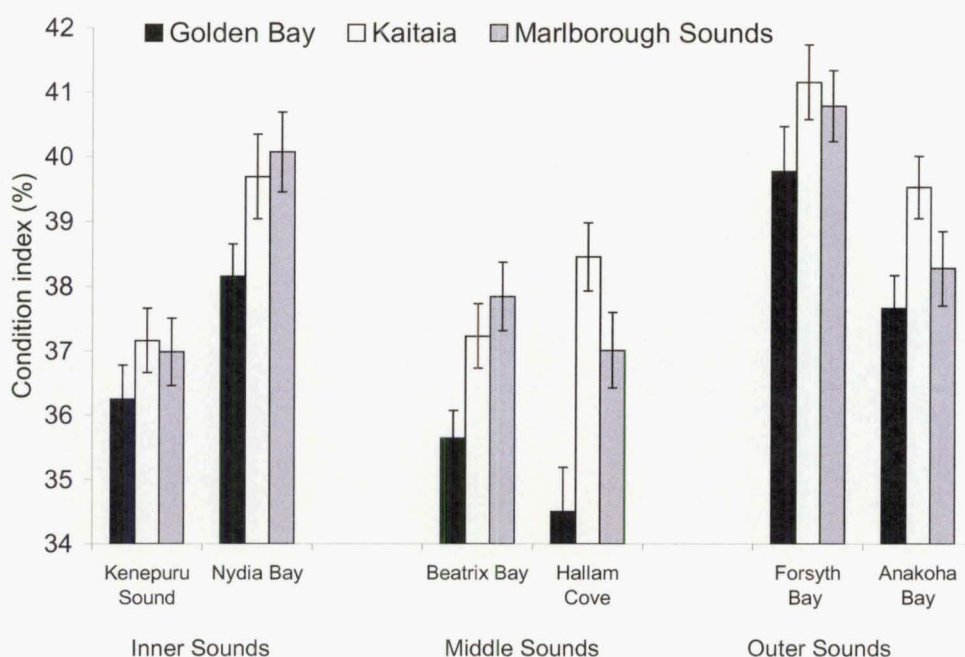


Figure 4.11. Mean condition of Golden Bay, Marlborough Sounds, and Kaitaia stocks at each of the six sites in Pelorus Sound during Trial 1. Bars = \pm 95% confidence intervals, $n = 800$ for each treatment.

Analysis of factors influencing condition in Trial 2 and 3

Time, Site (area), and Time \times site (area): The ANOVAs of condition data for Trial 2 and 3 showed that, as in Trial 1, temporal and spatial factors (and their interactions) accounted for most of explained (i.e. non-residual) variation mussel condition (Table 4.5b & c). Time, Site (area), and Time \times site (area) accounted for 15 and 21% of the total variation in condition in trial 2 and 3 respectively. As this trend is consistent with Trial 1, rather than describing the spatial and temporal patterns again, this section will focus on the stock effects, and determine whether the influence of stock (and its interactions) was consistent or predictable across the three trials.

Time \times stock: As in Trial 1, the time \times stock interaction was significant ($p < 0.05$) in Trial 3. The Golden Bay stock was generally in higher condition than the Kaitaia stock (up to 3%) following the mid-winter decline in condition (Figure 4.10c). Although there was some evidence that the Golden Bay stock was in lower condition than the Kaitaia stock before the mid-winter decline in condition in Trial 2 (Figure 4.10b), the Time \times stock term was not statistically significant ($p > 0.05$).

Site (area) × stock: This interaction indicated that certain stocks were in better condition than others at particular sites. In Trial 2, the Golden Bay stock was generally in lower condition than the Kaitaia and Marlborough Sounds stock; this difference was particularly large at Hallam Cove. In Trial 3, the pattern reversed and the Golden Bay stock was generally in higher condition than the Kaitaia stock, in this case the largest difference occurred at Beatrix Bay. It is notable that all of the mussels in Trial 2 were sampled prior to the mid-winter spawning period, while in Trial 3, most of mussels were sampled after the winter spawning period.

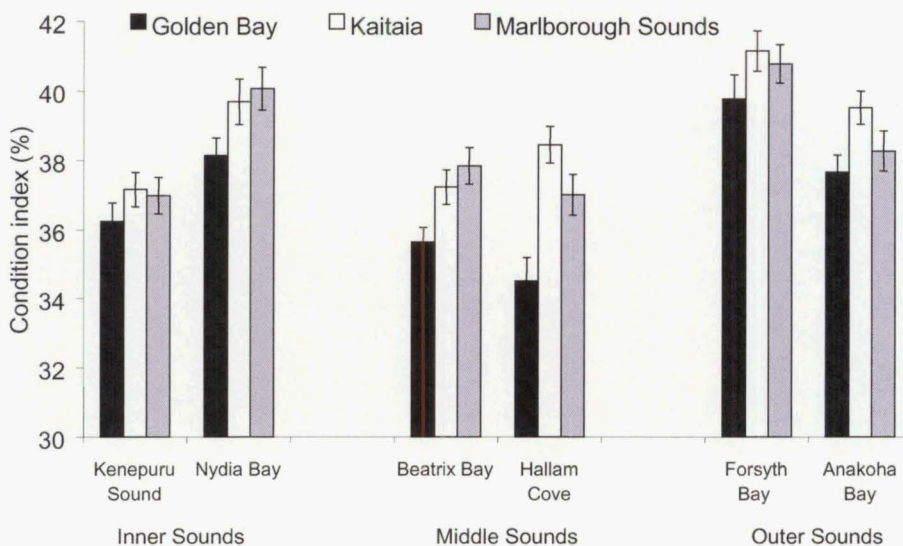


Figure 4.12. Mean condition of Golden Bay, Marlborough Sounds, and Kaitaia stocks at each of the six sites in Pelorus Sound during Trial 2 (January-May 1999). Bars = \pm 95% confidence intervals, $n = 240$ for each treatment.

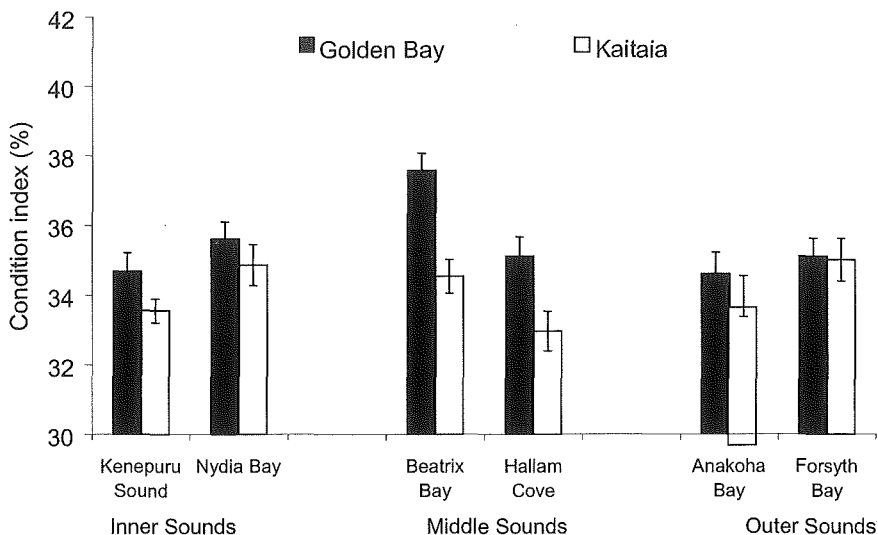


Figure 4.13. Mean condition of Golden Bay and Kaitaia stocks at each of the six sites in Pelorus Sound during Trial 3 (May-October 1999). Bars = \pm 95% confidence intervals, n = 240 for each treatment.

Time \times site (area) \times stock: As in Trial 1 the highest order interaction, of Time \times site (area) \times stock, was significant in Trial 2 and 3. This illustrated that at certain times and sites some stocks were in significantly higher condition than other stocks. This interaction is reflected in the plots of the differences in condition indices between stocks across spatial and temporal scales (Figure 4.14 & 4.15). In these plots the condition of Golden Bay and Marlborough stocks are compared against the Kaitaia stock, as the latter is the most common stock used in the mussel industry.

Although the differences in condition between the Golden Bay and Kaitaia stocks were small and variable, some generalizations can be made. From the beginning of the study until December 1998, the Golden Bay stock was often in higher condition than the Kaitaia stock (Figure 4.14). Between December 1998 and mid-June 1999 this pattern reversed and the Kaitaia stock tended to be in higher condition than the Golden Bay stock. From mid-June 1999 until the end of the study in October 1999, the Golden Bay stock was, again, generally in higher condition. There was no strong evidence to suggest that either of the stocks was consistently (i.e., throughout the year in all three trials) in higher condition at certain sites or areas

in Pelorus Sound, in all three trials. The change from the Golden Bay stock being in lower to higher condition than the Kaitaia stock in mid-winter (June/July 1999) coincided with a sharp decline in condition and reproductive maturity of all the mussels (Figure 4.7). Notably, there was no obvious change in the relative condition of the two stocks in March when mussels also spawned.

There were no clear patterns to the differences in condition between Marlborough Sounds and Kaitaia stocks (Figure 4.15).

At the completion of the experiments in October 1999, the density of mussels on the experimental dropper was measured. No significant differences ($p < 0.05$) in density were detected between stocks within the trials.

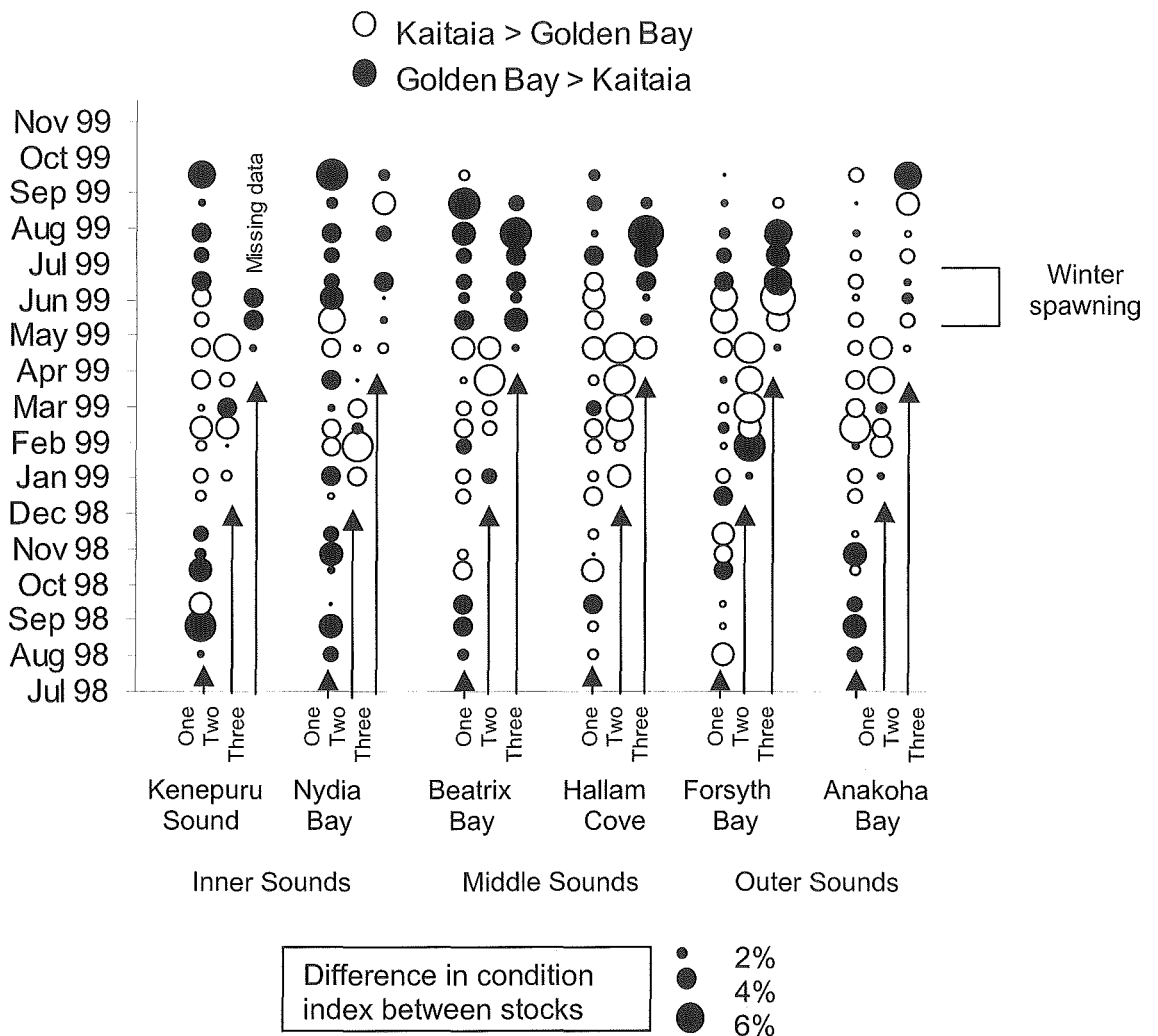


Figure 4.14. Differences in condition between the Golden Bay and Kaitaia stocks across spatial and temporal scales. Samples were collected at each of the 120 sites and times that mussels were sampled. Solid black circles indicate the Golden Bay stock was in the highest condition and white circles indicate that the Kaitaia stock was in the highest condition. Sites have been grouped by the area (inner, middle or outer sound) in which they are located. The size of the circle indicates the magnitude of the difference in condition index. One, Two, and Three specify the trial. Arrows point to when the sampling mussels in each of the trials began.

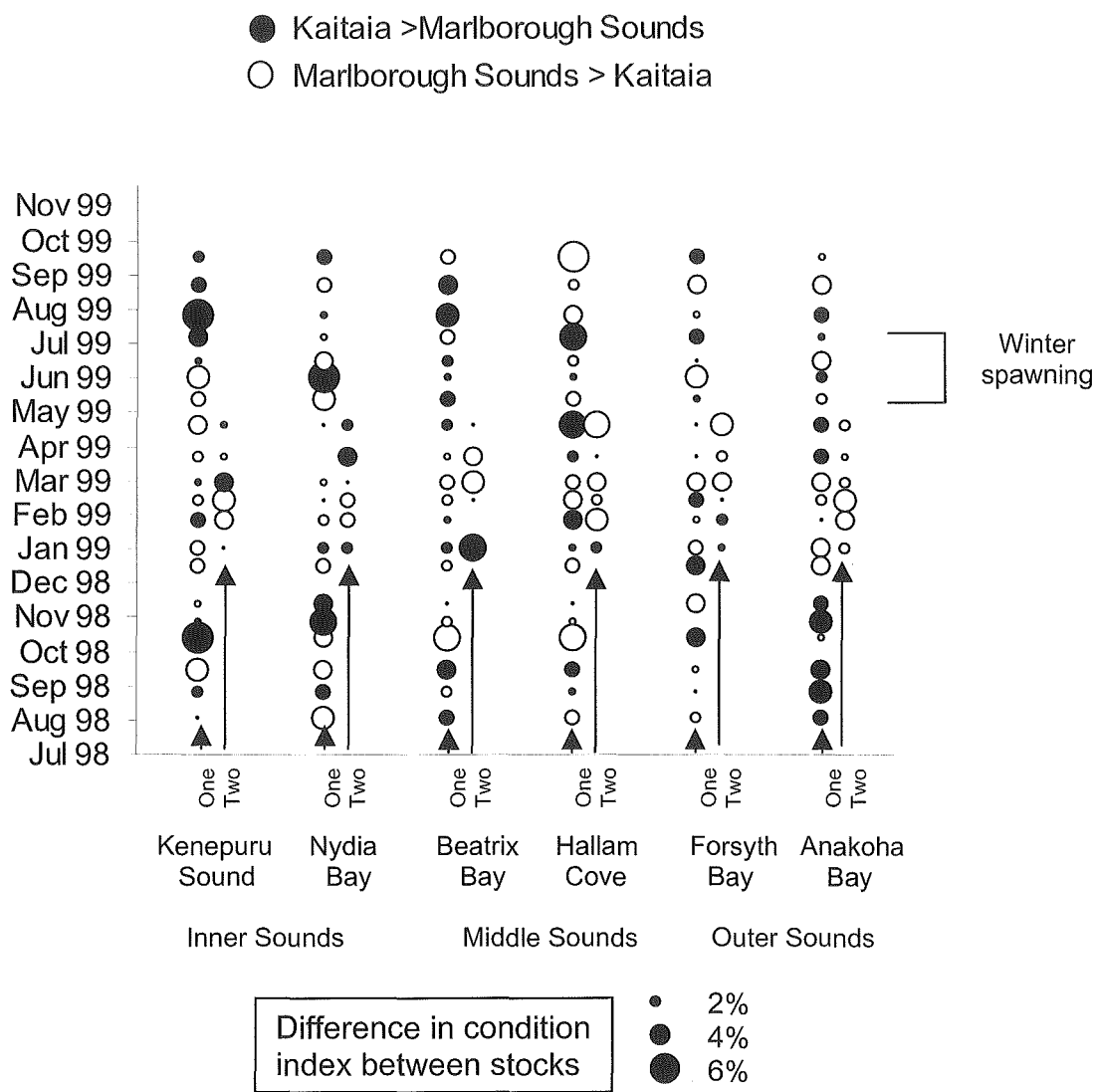


Figure 4.15. Differences in condition between the Marlborough Sounds and Kaitaia stocks across spatial and temporal scales. Samples were collected at each of the 120 sites and times that mussels were sampled. Solid black circles indicate the Marlborough Sounds stock is in the best condition and white circles indicate the Kaitaia stock is in the best condition. Sites have been grouped by the area (inner, middle or outer sound) in which they are located. The size of the circle indicates the magnitude of the difference in condition index. One and Two specify the trial. Arrows point to when the sampling mussels in each of the growth trials began.

4.4 DISCUSSION

4.4.1 The influence of stock on the condition of mussels

Stock did not influence the shell growth of mussels, but it did have a small and predictable influence on the condition cycles of Golden Bay and Kaitaia stocks in the three growth trials. The condition cycles were predictable in that prior to the winter spawning event in June/July the condition index of the Golden Bay stock was generally 1-4% lower than the Kaitaia stock. From immediately after the winter spawning event until the end of the study in October the pattern reversed and the Golden Bay stock was normally in 2-3% higher condition. This pattern is consistent with anecdotal observations made by mussel farmers in the Marlborough Sounds (Fox 1996). The results suggest small increases in condition of farmed mussels might be achieved by selectively harvesting the Golden Bay stock in the months following the mid-winter spawning event. The practicality of this technique is discussed in the General Discussion (Chapter 5), when the results from Chapter 3 are also taken into consideration.

Previous studies have suggested that stock can have a significant influence on the growth of mussels (Dickie *et al.* 1984, Mallet *et al.* 1987, Fuentes *et al.* 1994, Perez Camacho *et al.* 1995). However, as outlined in the introduction, these studies have two major shortcomings: the mussel stocks were subjected to different environmental conditions prior to studies, and the studies were not repeated. As a consequence, there has been debate on whether the differences in growth are due to true stock effects (i.e., genetically mediated) or are due to physiological adaptations to the previous environment (Mallet *et al.* 1987, Fuentes *et al.* 1992, Perez Camacho *et al.* 1995). It is also unclear whether the same stock-related traits would consistently occur if the studies were repeated. This is an important consideration; for mussel farmers to exploit a stock-related trait, the trait must consistently occur within the stock.

The present study is unique as the growth of mussels stocks was compared in three trials and the environments that the stocks were exposed to before the trials were controlled. These results suggest the differences in the condition cycles of the Golden Bay and Kaitaia stocks were relatively consistent features of the stocks and

were probably genetically mediated. Although there was a pattern to the differences in condition between the Golden Bay and Kaitaia stocks, this did not occur between the Kaitaia and Marlborough Sounds stocks.

The absence of any clear cyclical differences in condition cycle of the Marlborough Sounds and Kaitaia stocks, in this study, may be related to the level of mixing (or hybridisation) between the stocks (Figure 4.16). Large amounts of Kaitaia spat have been imported into the Marlborough Sounds over the last 25 years (Hickman 1992) for use in aquaculture. It is probable that spat caught in the Marlborough Sounds consist of either second-generation Kaitaia stock, true (wild) Marlborough Sounds stock, or variable combinations of the two stocks. These different scenarios may mask any differences in condition cycle that may have once existed between the Marlborough Sounds and Kaitaia stocks. In contrast to the Marlborough Sounds, Golden Bay has historically been a net producer of spat and only relatively small amounts of Kaitaia spat have been transplanted into the area for ongrowing. Less mixing between the Golden Bay and Kaitaia stocks may have allowed unique traits (such as condition cycles) to persist in the Golden Bay stock.

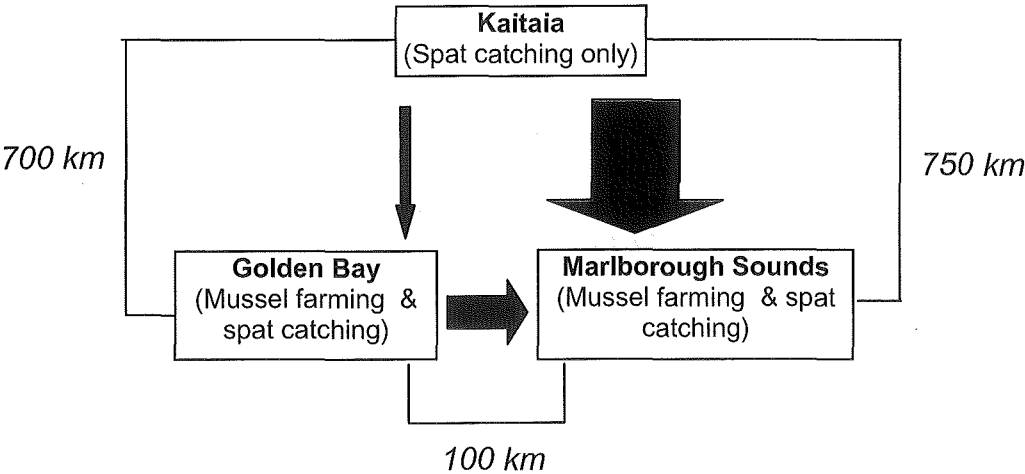


Figure 4.16. Locations between which spat are transported for use in mussel farming. The sizes of the solid black arrows indicate the relative volume of spat moved between spat catching and farming areas. Distances between spat catching and farming locations are italicised.

The extent to which natural mixing (i.e., not involving the movement of spat for use in aquaculture) occurs between geographically distant populations (or stocks) of

P. canaliculus has been actively debated in the scientific literature (see Smith 1988, Gardner *et al.* 1996a & b, Apte & Gardner 2000). Most studies have found that gene flow is restricted between populations (Smith 1988, Sin *et al.* 1990, Gardner *et al.* 1996a & b). However, in the most recent, and largest study no significant differences were found between 35 populations of *P. canaliculus* from around the New Zealand coast (Apte & Gardner 2001). Apte and Gardner argued that it was likely that all *P. canaliculus* mussel populations are genetically homogenous because spat are probably widely distributed due to their 3-5 week pelagic larval stage (Hayden 1995).

Although this rationale seems reasonable, genetic differences do occur between populations, despite mixing. The best-studied example involves the maintenance of different LAP⁹⁴ allele frequencies in *M. edulis* populations due to allele-dependent mortality (Koehn *et al.* 1976, 1980, Lassen & Turano 1978, Thesien 1978, Gardner-Kepkay *et al.* 1983, Hilbish 1985). For example, in Long Island Sound (USA), clines in LAP allele frequency occur along the salinity gradient between the open sea and the inner sound. Lap⁹⁴ alleles exist at the highest frequency (c. 0.55) in high-salinity environments, and decrease in frequency (to c. 0.12) in lower salinity environments. The LAP⁹⁴ alleles directly influence the ability of mussels to osmoregulate and survive at different salinities (Hilbish *et al.* 1982). As a consequence, mussel larvae originating from oceanic sites have higher mortality rates and reduced growth when settling in estuarine areas (Hilbish 1985). It is important to note that in these LAP allele studies selection did not totally prevent the mixing, but rather helped maintain unique traits within the populations. Selection could explain the persistence of unique traits in Kaitaia and Golden Bay stocks, despite some mixing of stocks (both natural and human mediated).

Smith (1988) proposed that the genetic differences between populations of *P. canaliculus* in northern and southern New Zealand might reflect adaptations to different thermal environments. An adaptation to cooler water temperatures could explain why the Golden Bay stock is generally in higher condition than the Kaitaia stock following the winter spawning event when water temperatures are low.

4.4.2 The Influence of spatial and temporal factors on mussel growth

Spatial and temporal factors were more important than stock in determining the growth of mussels in Pelorus Sound. For example, at a single sampling time the maximum range in condition indices between experimental sites was 23%, while the maximum range between stocks was 7%. Site was also important in determining how quickly mussels recovered condition following the winter spawning event. The most rapid gain occurred at Beatrix Bay, where condition rose from a low of 29% in July to 36% in August (Figure 4.11). In contrast, the condition of mussels at Anakoha Bay declined from 30% to 28% over the same period. These differences in recovery following spawning are almost certainly linked to differences in phytoplankton abundances, which are in turn controlled by nitrogen availability, light, water column stability, and grazing (Carter unpublished, Gibbs & Vant 1997, Ross *et al.* 1998, Ogilvie 2000). It is reasonable to assume that if phytoplankton abundances could be enhanced following winter spawning the condition of harvested mussels could also be significantly improved. This possibility is discussed in detail in Chapter 5.

It was clear that the condition of mussels at some sites could change radically through time, and these changes were often independent of any seasonal cycle. For example, in the middle sounds the mean condition index of mussels declined from c. 50 % in August 1998, to < 35% in February 1999. Intuitively, these changes in condition are linked to food abundance, as phytoplankton can also vary on similar spatial and temporal scales in the Sound (Ross *et al.* 1997b, Carter pers. comm., May 2003). Difficulties arise, however, in correlating the observed changes in mussel condition to measures of phytoplankton abundance (see section 3.4.2 for a discussion).

This study suggests it is not really correct to classify certain farms, or even areas of the Sounds as better locations to grow mussels, because condition and commercial yields are dynamic through time. This strong spatial and temporal variation in the condition of farmed mussels in Pelorus Sound also indicate that the amount of mussels that parts of the Sound (or the whole Sound) can sustain also change through time. This is an important factor for managers to consider as an

additional 7,785 ha of mussel farms are currently being evaluated for future development in or around the Marlborough Sounds.

Chapter 5

General Discussion

5.1 INTRODUCTION

Mussels are an important group of animals in both freshwater and marine ecosystems. They are adaptable (Marsden & Weatherhead 1999), fast growing (Rivonker *et al.* 1993), efficient filter feeders (Hatton 1999), and are often highly abundant and dominant in many habitats (Morton & Miller 1973, Blodgett 1992, Svane & Ompi 1993, Jeffs *et al.* 1999). Because of their ecological importance, many aspects of the biology of mussels, including their distribution, feeding behaviour, genetics, and role in food webs have been extensively studied (Riessen 1991, Menge *et al.* 1994, Hawkins *et al.* 1999, Gardner 2000, Apte & Gardner 2001). In recent years, as the commercial importance of mussel aquaculture has grown, an increasing amount of research has been directed towards understanding the growth of farmed mussels (Hickman 1979, Wallace 1980, Hickman *et al.* 1991, Fuentes *et al.* 2000).

Studies have demonstrated that the growth of farmed mussels may vary between locations, through time, and between stocks (see Table 1.1 for a summary). The problem with previous studies, and particularly those investigating the influence of stock, is that the environment that the mussels were exposed to before the experiments were not controlled. In addition, the studies were not replicated or repeated. As a consequence it is unclear if the same stock, caught at different times, would exhibit the same trait. To be commercially useful, a stock-related trait (e.g., higher growth) must be predictable. The present study is the first to expose mussel stocks to identical conditions prior to experiments and the first to repeat experiments in order to determine the predictability of traits.

This research on the growth of *P. canaliculus* stocks is of practical significance as it provides the opportunity to understand and possibly minimise the problem that the Marlborough Sounds mussel industry has obtaining well-conditioned mussels in mid-winter. Anecdotal evidence from marine farmers suggested that the Golden Bay and Marlborough Sounds stocks remain in better condition than the more commonly used Kaitaia stock (Fox 1996). If so, it might be possible to harvest the Golden Bay and Marlborough Sounds stocks selectively over winter to increase the condition of mussels. The identification of locations or stocks with overall growth rates is also of

interest as this would decrease crop rotation time and increase the profitability of marine farming.

The specific aims of the study were to determine

1. Why mussels are in poor condition over winter;
2. Whether different mussel stocks have different growth rates and condition cycles when they are grown at the same location;
3. Whether traits associated with stocks occur regardless of the environment they are exposed to early in life, or the timing of spat capture;
4. Whether certain stocks of mussels grow better in particular areas of Pelorus Sound;
5. Whether differences in growth between stocks are significant when compared to spatial and temporal factors;
6. How the knowledge gained in this study be used increase yields in harvested mussels.

As many of the outcomes from these aims were interconnected, the aims are not necessarily addressed sequentially in this chapter.

5.2 THE MID-WINTER DECLINE IN CONDITION

Between June and July in both 1998 and 1999 mussels at all six experimental sites declined in reproductive maturity and condition. This indicates that farmed mussels in Pelorus Sound are in poor condition over winter because they spawn (Aim 1). Poor meat yields during winter also occur in other important mussel farming regions of the world, including Spain (Navarro *et al.* 1991, Caceres-Martinez & Figueras 1998), the Netherlands (Pieters *et al.* 1980), Canada (Mallet & Carver 1989, Mallet *et al.* 1978), and the United Kingdom (Dare & Edwards 1975, Bayne & Widdows 1978, Stirling & Okumus 1995). In these regions, however, the poor yields are due to a negative scope for growth (SFG) caused by a combination of low food levels and the initiation of gametogenesis (Dare & Edwards 1975, Navarro *et al.* 1991, Okumus & Stirling 1998). Although mid-winter spawning is unusual in mussels it is not unique to *P. canaliculus*. In South Africa, populations of intertidal *Perna perna* have also been observed to spawn (and settle) in mid to late winter (Berry 1978). The

present study is, however, the first to identify the cause of the mid-winter decline in condition of farmed *P. canaliculus* in the Marlborough Sounds.

With the exception of the winter spawning event, the reproductive cycles of mussels in the present study were similar to those seen in wild and cultured populations of *Mytilus* spp, (Wilson & Seed 1974, Rodhouse *et al.* 1984, King *et al.* 1989, Villalba 1995) and wild populations of *P. canaliculus* (Buchanan 1998). This involves gametogenesis in late winter and reproductive maturity through spring, summer, and autumn (Wilson & Seed 1974, Rodhouse *et al.* 1984, King *et al.* 1989, Villalba 1995). The large proportion of farmed *P. canaliculus* that were mature between spring and autumn is also consistent with studies that have found peak recruitment in Pelorus Sound during the same period (Hayden & Kendrick 1992, Hayden 1995, New Zealand Marine Farmers and Sealord Shellfish Ltd. spat monitoring programs).

Many attempts have been made to understand the environmental variable or variables controlling the reproductive cycle of mussels (e.g., Newell 1982, Bayne *et al.* 1983, Thompson, 1984, Caceres-Martinez & Figueras 1998). Water temperature and food availability are usually cited as the most important factors controlling maturation (Seed 1976 and Bayne 1976 for Reviews, Seed & Suchanek 1992). The suggestion that water temperature is important stems primarily from studies in the Northern Hemisphere that have found spawning in *Mytilus* spp occurs earlier in southern populations than in northern populations (Seed 1975, Bayne 1976 for a review). Similarly, Bayne (1975) found a linear relationship between the rate of gametogenesis and degree-days for populations of *M. edulis* in the United Kingdom.

However, significant differences in the reproductive maturity still do occur between mussel populations exposed to identical water temperatures (Newell *et al.* 1982). In these situations food supply appears to play an important role in the size, the timing, and the duration of spawning events (Thompson 1979). Biochemical studies suggest the timing and magnitude of spawning is related to the amount of glycogen deposited during periods of phytoplankton abundance and the subsequent conversion of these reserves to lipids during maturation (Gabbott 1975, Pieters *et al.* 1976, Zandee *et al.* 1980). Food supply appears to determine whether mussel

populations recover adequately following a spring spawning to allow a subsequent spawning in summer or autumn (Newell *et al.* 1982). Newell *et al.* (1982) suggested this opportunistic approach to gametogenesis allows mussels to capitalise on high phytoplankton levels that maximise both the survival of the planktotrophic larvae and the recovery of adults. These studies indicate that the high level of reproductive maturity and condition of mussels in early winter in Pelorus Sound is a result of high levels of phytoplankton. This is supported by a long-term study in Beatrix Bay that has shown phytoplankton biomass often remains high through to early winter (Gall *et al.* 2000).

Conflicting opinions exist on the precise factors that stimulate the spawning of mussels. Under laboratory conditions a broad range of techniques including heat shock, serotonin injection, and agitation can, at times, stimulate the spawning of *P. canaliculus* (Redfearn 1998, Buchanan 1999). However, the success of stimuli often varies between studies. For example Tortell (1980) was unable to stimulate spawning in *P. canaliculus* using heat shock, which both Buchanan (1998) and Redfearn (1998) successfully used.

The search for factor(s) that induce spawning in wild mussel populations is made complex by the range of stimuli that have been implicated, and because many of the potential stimuli co-vary (e.g., water temperature and day length). Strong wave action, lunar cycles, desiccation, salinity changes, changes in day length (season), and rapidly changing water temperatures have all been implicated (see Bayne 1976 for a review). Other studies have also found spawning to occur with no obvious stimuli (Bangli 1978, Tortell 1980) other than the mussels being mature. Considering the broad range of results from these studies it seems likely that when mussels are reproductively mature, any of several, even subtle changes in the environment can stimulate spawning.

In the current study, winter spawning, as indicated by the decline in condition, occurred simultaneously at all six sites. Spawning coincided with rapidly declining and near minimum water temperatures and day lengths. Simultaneous declines in the condition of *P. canaliculus* have previously been recorded at several locations along the length of New Zealand in mid-winter (Hickman & Illingworth 1980, Hickman *et al.*

1991). Because several of the sites in Hickman's 1980 study were separated by several hundred kilometres, a specific water temperature does not appear to be the stimulus to spawning. This suggests either rapidly declining water temperatures or a stimulus associated with changing day length synchronised and stimulated spawning in mid-winter.

On average, the meat weight of farmed mussels declined by c. 20% during mid-winter spawning in 1998 and 1999 (declining from a mean of 16.37g in June to 13.07g in July). Considering the biomass of mussels the Sound, it appears several thousand tonnes of gametes are released during winter spawning. It is, therefore, a paradox that no significant spat settlement occurs in Pelorus Sound in late winter (Hayden & Kendrick 1992, Hayden 1995, Mussel Industry spat monitoring program).

The issue of spat fall and spat catching is perplexing. Despite tens of thousands of tonnes of mussels being cultivated in the Pelorus Sound, farmers have difficulties catching adequate volumes of spat in the area. In contrast, in Golden Bay less than 100 km away, fewer mussels are cultivated, but spat falls are larger and more consistent (Sealord Shellfish Spat Monitoring Program). This raises the question of whether commercial spat catches in the Marlborough Sounds and Golden Bay originate primarily from wild or farmed populations of *P. canaliculus*. Redfearn (1988) suggested that farmed mussels might not be producing a large amount of viable spat. Using a series of laboratory experiments, he found that although brood stock obtained from farms in the Marlborough Sound could be induced to spawn, very few spat survived to settlement. The absence of a spat settlement associated with the winter spawning of farmed mussels is consistent with Redfearn's idea that farmed mussels, for some unknown reason, are not producing viable larvae.

Considering the problems that the Marlborough Sounds mussel industry has catching spat and the difficulties researchers have had producing spat in hatcheries (using farmed brood stock) it would be worthwhile to determine if the viability of larvae differs between wild and farmed mussel populations.

5.3 UNEXPLAINED VARIATION WITHIN ANOVA MODELS

Most of the variation in the shell growth rate and condition ANOVA models was unexplained (i.e. 43-99%). This was not expected as the factors included in the models (Time, Area, Site(area), and Stock and their interactions) had previously been identified as important influences on the shell growth and condition of bivalves (see section 2.2).

Despite individual factors explaining only a small amount of variation, many of significant factors were commercially important. This was particularly evident in the second study where the factor “Time x area” was significant but only accounted for 5% of the total variation in mussel condition. The identification of “Time x area” as a significant factor is commercially relevant as it highlights the importance of selecting the right place (i.e. area) at the right time to harvest. For example, in August 1998 mussels grown in the Middle Sound were in very high condition (c. 50%), and mussels in the Outer Sound were in very low condition (c. 25%) (Figure 4.9). At this time the yield of live mussels¹ from a longline in the Middle Sound would have been approximately five tonnes (worth c. \$6500) higher than in the Outer Sound.

5.4 DIFFERENCES IN SHELL GROWTH BETWEEN STOCKS

The shell growth rate of the Golden Bay stock was significantly higher than either the Kaitaia and Marlborough Sounds stocks in the first experiment (Chapter 3). There were, however, no differences in shell growth rate between any of the stocks when the growth trial was repeated three times in Chapter 4. There are two possible explanations for the different results. First, the higher growth of the Golden Bay stock in Chapter 3 was a true stock-related trait (with a genetic basis), but the trait doesn't always occur in the Golden Bay stock. The second possibility is that the environment that the mussels were exposed to prior to the start of the experiment in Chapter 3 caused the differences in growth. These two possibilities are discussed below.

Significant genetic variation can occur within mussel stocks (Gosling and Wilkins 1985, Hilbish 1985, Smith 1988). For example, Gosling (1985) found variations in the allozyme frequencies between cohorts of *M. edulis* settling in Killary

¹ Eighty five millimetre mussels grown at 170 mussels per metre on a 4000 metre of culture rope.

Habour on the west coast of Ireland. Selection was suggested as a cause for these differences. It is possible that selection could lead to genetically mediated differences in the growth of *P. canaliculus* caught at the same location at different times. It is notable, however, that differences in shell growth occurred only when the environment that the stocks were exposed to prior to the experiments was not controlled (i.e., in Chapter 3). This tends to suggest the differences in the early growing environment were responsible for the variations in shell growth in Chapter 3.

The environmental conditions to which mussels are exposed prior to being transplanted to a new location have the potential to influence their subsequent growth. As outlined in Chapter 3, mussels can modify their feeding behaviour to maximise their food intake and growth, and these adaptations may persist for at least several months (Bayne *et al.* 1984, 1987, Widdows *et al.* 1984, Marsden & Weatherhead 1999). It is likely that the mussel stocks used in the first study (Chapter 3) were exposed to different environmental conditions (i.e., phytoplankton abundances) as they were grown on four different farms prior to being transferred to the experimental sites. Because differences in shell and meat growth only occurred between stocks in the first study (Chapter 3), the early growing environment is a possible cause for the differences in growth. This study indicates the growth of stocks may be influenced by the environment they are exposed to early in life, or when they are caught (Aim 3). This has implications for the interpretation of stock-studies that have been carried out in other important mussel farming areas including Canada, Spain, and United Kingdom (Dickie *et al.* 1984, Mallet *et al.* 1987, Mallet and Caver 1989, Fuentes *et al.* 1992, 1994, Stirling and Okumus 1994, Perez-Camacho *et al.* 1995, Okumus and Stirling (1998). In all of these studies, the environments that the stocks were exposed early in life were different. As a consequence, the results should be considered preliminary until the studies are repeated and/or the early growing environment that the stocks are exposed to are controlled.

As the differences in shell growth between stocks in many studies have been large and commercially significant (e.g., a 25% difference in the present study) further research on the influence of early growing environment is justified.

5.5 THE INFLUENCE OF STOCK ON CONDITION

Stock had a small, but predictable influence on the condition cycles of Golden Bay and Kaitaia stocks in all four trials. The influence of stock was predictable in that prior to winter spawning the Kaitaia stock was in better condition than the Golden Bay stock. Following winter spawning this pattern reversed and the Golden Bay stock was in better condition. This study confirms that some mussel stocks do have different condition cycles when grown at the same location (Aim 2). But the study also indicates that making practical use of these differences would be difficult for three reasons.

First, the gains achieved by selectively harvesting stocks would be small. The mean condition index of the Golden Bay stock following spawning in July was only 2% higher than the Kaitaia stock (Figure 5.1). By selectively harvesting the Golden Bay stock in July and the Kaitaia stock for the rest of the year, the mean annual condition of harvested mussels would only be c. 0.2% (i.e., $2\% \times 1/12$) better than harvesting only the Kaitaia stock. This is only 1/12 of the 2% increase in mean annual condition described in the General Introduction, and would produce only a minor improvement in yield. For example, on a longline containing 33 tonnes of mussels, an improvement in condition from 38% to 38.2% (CWI) would increase the total yield of live mussels by c. 132 kg. This would be worth about \$158 at the current (2002) price of \$1200 per tonne. A large proportion of this increased production would be offset by the higher cost of obtaining Golden Bay spat.

The second reason is that the response of stocks varied between sites and trials. For example, in August the condition index of the Golden Bay stock ranged from 4% better to 4% poorer than the Kaitaia stock (Figure 5.1). There was no evidence, however, that particular stocks consistently (i.e., in all four trials) outperformed other stocks in certain areas of Pelorus Sound (Aim 4). As a result, there is no advantage seeding farms with a specific stock on the basis of its location. This is in contrast to anecdotal evidence that suggested the Golden Bay stock is generally in higher condition than the Kaitaia stock in the outer Sound (Fox 1996). This variability between sites means it would be difficult for farmers to predict the size of the gains

they might achieve by selectively harvesting stocks, or even whether they would consistently achieve gains.

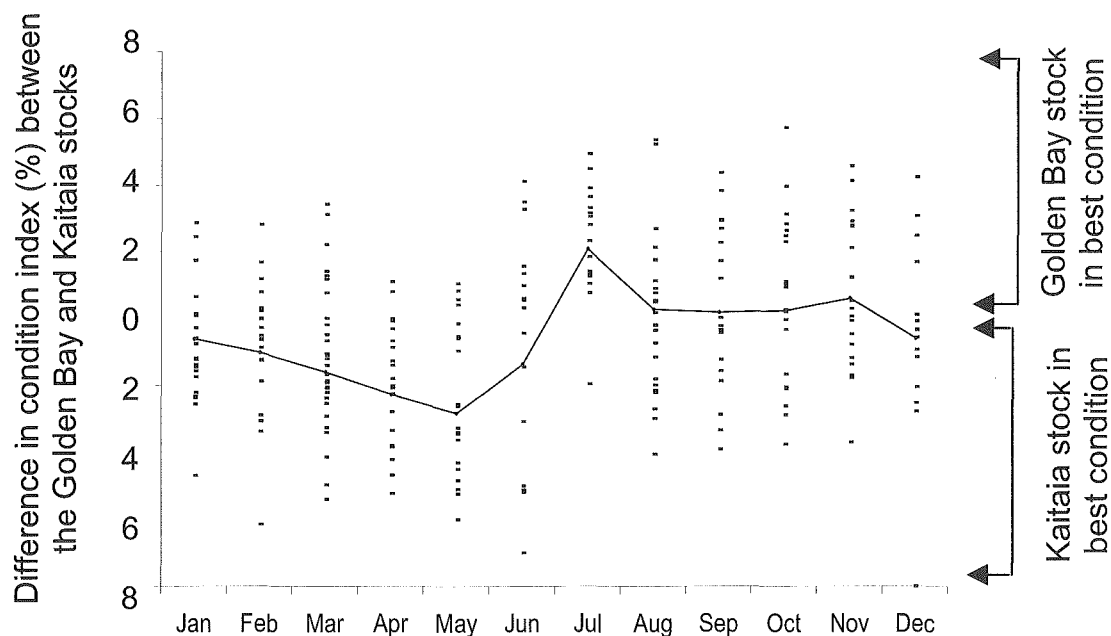


Figure 5.1. Difference in condition between the Golden Bay and Kaitaia stocks. Data from all four trials are displayed and grouped by month. Each data point represents the mean difference in condition index between the two stocks at one site in one of the four trials. The solid line indicates the mean difference in condition between the stocks. For example, in July the mean condition index of the Golden Bay stock was 2% better than the Kaitaia stock.

The third difficulty in making practical use of combinations of stocks is linked to predicting the length of time that stocks will remain in better condition. This varied between trials. In the trials described in Chapter 4 the condition index of the Kaitaia stock was better than the Golden Bay stock between April and the mid-winter spawning event. From immediately after spawning until the end of the study in October, the condition index of the Golden Bay stock was better than the Kaitaia stock (Figure 4.14). In contrast, in the trial in Chapter 3 the condition of the Kaitaia stock was generally better than the Golden Bay stock for a longer period, between January and the winter spawning event. Immediately after spawning, the Golden Bay

stock was in better condition than the Kaitaia stock only for a brief period, between July and August (Figure 3.10).

The different results in Chapter 3 and 4 were, at least in part, an artefact of the rapid shell growth (relative to meat growth) of the Golden Bay stock in Chapter 3. Therefore, in order to fully predict the differences in the condition cycles of the Golden Bay and Kaitaia stocks it is essential to understand what caused the higher shell growth of the Golden Bay stock in Chapter 3. This further justifies research on the influence of prior environment on the growth, and particularly the shell growth of mussels.

Because of these three factors I believe it is not feasible to develop a harvesting regime involving Golden Bay and Kaitaia stocks that would enhance the yield of farmed mussels by a substantial or predictable amount (such as the 2% discussed in the General Introduction).

5.6 SPATIAL AND TEMPORAL INFLUENCES ON MUSSEL CONDITION

The location where mussels were grown and the time of sampling were the most important factors influencing the condition of mussels. For example, the largest range in condition between sites at a single time was 23% (August 1998) and the largest range in condition between times within a single site was 22% (Hallam Cove). In contrast, the largest difference in condition between stocks was 7% (between the Golden Bay and Kaitaia stocks caught in the spring of 1997 and sampled in June 1999). These results show that spatial and temporal factors are much more important than stock in determining the condition of farmed mussels in Pelorus Sound (Aim 5). This is consistent with the findings of Okumus & Stirling (1998) who are the only other researchers to investigate the relative importance of stock, site, and time of harvest on the condition of farmed mussels. By cross-transplanting mussels between two Scottish sea lochs they found significant differences in condition between lochs and times of harvest, but only occasional differences between stocks within lochs.

The relatively large range in condition between sites in Pelorus Sound is commercially useful as it ensures that well-conditioned mussels (c. 38%+) are normally available in Pelorus Sound for most of the year. From a management

viewpoint, the more farms that processors have the option to harvest from, the better the yields they are likely to achieve. Ideally this would include farms located in different areas of Pelorus Sound, as sites within areas often have similar condition cycles (Figure 3.6, 4.9).

Although this strategy would be effective for most of the year, it would not help immediately following mid-winter spawning when mussels are consistently in poor condition throughout the Sound. The current study, and a review of previous studies suggests a period of poor condition in mid-winter is a consistent, and perhaps inevitable, feature of the condition cycle of farmed mussels Pelorus Sound (Hickman & Illingworth 1979, Hickman *et al.* 1991).

The rate at which mussels recover from the mid-winter spawning event does, however, vary between areas and years. In the first study mussels located in the middle sound area (Beatrix Bay and Hallam Cove) increased in condition from c. 29 to 42% over approximately five weeks following spawning. In contrast, in the second study condition remained low ($\leq 35\%$) at all of the sites over the same period. The rates at which mussels recovered condition in 1998 and 1999 influenced commercial harvests (Figure 1.5 Chapter 1). In 1998, when condition recovered rapidly following spawning, mussel harvesting quickly rebounded to pre-spawning levels. In 1999, when condition remained low following spawning, harvests also remained low.

This study demonstrated that the best way for mussel farmers and processors to minimise the impact of the mid-winter decline in condition and maximise the yields of farmed mussels is exploit the high degree of spatial and temporal variation that occurs in mussel condition. This would involve growing mussels across as wide a range of geographic areas as is feasible, and then closely monitoring condition in order to identify locations (and in particular areas) where condition indices are the highest (Aim 6).

5.6.1 Artificial fertilisation and phytoplankton production

The condition and growth of mussels has been directly related to phytoplankton abundance (Newell *et al.* 1982, Spencer *et al.* 1986, Utting 1993 Perez-Camacho *et al.* 1995). If phytoplankton abundances could be enhanced when

mussels are recovering from the mid-winter spawning event, it would be expected that the condition indices and yields from farmed mussels could be significantly improved. Phytoplankton growth is often limited by the availability of essential nutrients (Coale *et al.* 1996, Gibbs & Vant 1997, Boyd *et al.* 2000, Gall *et al.* 2001a&b). In Pelorus Sound, nitrogen in the form of nitrate or ammonia is the key nutrient limiting phytoplankton abundance (Gibbs & Vant 1997, Ross *et al.* 1998b, Ogilvie 2000, C. Carter, pers. comm. April 2002). Elevating ambient nitrogen levels to c. $100 \mu\text{gL}^{-1}$ can result in up to a 13 fold increase in phytoplankton abundance in as little as two days (Gibbs & Vant 1997). These increases in phytoplankton abundance can be achieved, during most of the year (Gibbs & Vant 1997, Ross *et al.* 1998b, Ogilvie 2000, C. Carter, pers. comm. April 2002), including August when mussels are attempting to recover from spawning (C. Carter, pers. comm. April 2002).

Two approaches could be used to increase the phytoplankton available to farmed mussels in Pelorus Sound. First, nitrogen could be added directly into the Sound. Second, phytoplankton blooms could be induced in large enclosures (such as a closed off bay or large pond) and mussels could moved to, and fattened, in these areas prior to harvest.

Major ethical, ecological, and practical issues would need to be addressed before an attempt to add nitrogen directly to Pelorus Sound could be considered. In addition to the required consultation and resource consents the following important questions would need to be answered.

Would nitrogen disperse too rapidly to have a significant influence on phytoplankton abundance? Strong currents in Pelorus Sound (Heath 1974, 1976a) have the potential to flush nitrogen from a bay before it is utilised by phytoplankton.

Would the algal community that develops be predictable? Fertilisation can lead to significant changes in the composition of phytoplankton communities (De Pauw 1983, Ogilvie 2000, Gall 2001a). Studies in Pelorus Sound suggest diatoms such as *Skelotemena* spp. and *Chaetoceros* spp. show the largest increase in abundances following the addition of nitrogen (Ogilvie 2000, C. Carter, pers. comm. June 2003). It would be important to determine whether these species always dominate or whether the initial phytoplankton community or the prevailing environmental conditions

influence the subsequent community that develops. If different species dominate it would be essential to determine whether they are useful sources of food for mussels or include toxic or problem species. The development of a toxic bloom following fertilisation is an obvious concern, but other adverse effects associated with algal blooms also need to be considered. These include asphyxiation of marine life caused by oxygen depletion (Holmes & Lam 1985, Jones & Rhodes 1994); gas bubble trauma from extreme oxygen supersaturation (Renfro 1963); chemical toxicity caused by ichthyotoxins (Roberts *et al.* 1983, Black *et al.* 1991); mechanical damage to fish gills caused by the spines of algae such as *Chaetoceros* spp. (Yang & Allbright 1992); and increased seawater viscosity due to the secretion of mucilages (Hallegraeff 1992). Macroalgae may also increase in abundance (Bowen & Valiela 2001) and lead to the excessive biofouling of mussel farms and the clogging of farm machinery.

In addition it is unclear how grazers, other than mussels, might respond to increased primary production following fertilisation. Bradford *et al.* (1987) has suggested zooplankton grazing may play an important role in controlling phytoplankton in Pelorus Sound. It is possible that zooplankton may suppress any increased primary production that results from fertilisation.

Many of the issues associated with adding nitrogen directly to Pelorus Sound could be avoided, or more easily controlled, by instead fertilising large enclosures and using these to fatten mussels prior to harvest.

Several studies have demonstrated it is feasible to enhance primary production and accelerate the growth and condition of juvenile bivalves (<30 mm) in large ponds (Guerrero Valero *et al.* 1981, De Pauw *et al.* 1983, Strand 1996). For example, by fertilising a 67 000 m³ landlocked pond in Norway, Strand (1996) enhanced *Ostrea edulis* growth by 600%. Similar, but larger scale operations offer the potential to increase the condition and yields of farmed *P. canaliculus* in Pelorus Sound following mid-winter spawning, and for much of the year.

5.7 SUMMARY AND COMMERCIAL IMPLICATIONS

This has been the first study to investigate the relative importance of time of harvest, culture location, and geographic origin on the growth of farmed *P.*

canaliculus. The study was unique, as it is the only research that has used multiple growth trials to determine whether the same traits occur in stocks caught at different times. It has also been the only study to control the environment that mussel stocks were exposed to in early life, and the first investigation to identify why farmed *P. canaliculus* decline in condition during winter.

The overall conclusion of this research is that, although stock has a significant influence on the condition cycle of farmed *P. canaliculus*, time of harvest and culture location are the key determinants of condition and commercial yield. This highlights the importance of identifying the “right” place at the “right” time to harvest mussels.

Mussel farmers are advised to locate farms across a broad range of areas in Pelorus Sound and closely monitor the condition of mussels through time. This will allow them to exploit the high degree of spatial variability in mussel condition, to minimise the impact of winter spawning events, and therefore maximise yields throughout the year.

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APPENDIX 1

Length and condition frequency distributions

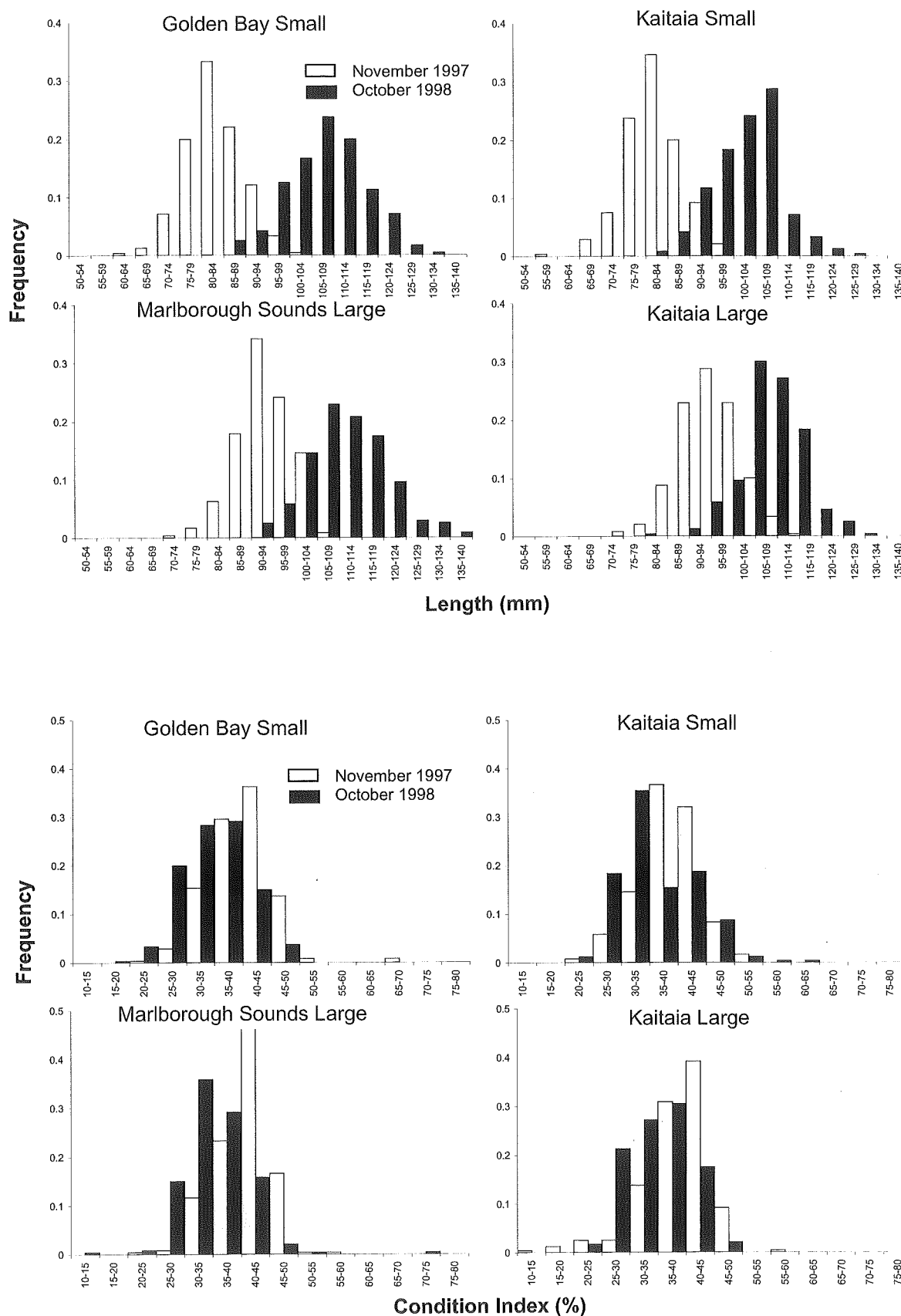


Figure 1 Length and condition index frequency distributions for mussel stocks at the start (1 November 1997) and end (5 October 1998) of the first study.

APPENDIX 2

Influence of mussel shell length on condition index

The relationship between the condition indices and shell lengths of mussels sampled during the study are plotted on Figure 1. Shell length explained less than 2% of the observed variation in condition. In addition, the slope of the regression was close to zero (0.027), indicating any influence shell length did have on condition was small (i.e. a c. 0.27% difference in condition index for mussels with a 10 mm difference in length). Shell length was therefore discounted as an important influence on the condition of mussels, and the condition of large and small mussel stocks were compared.

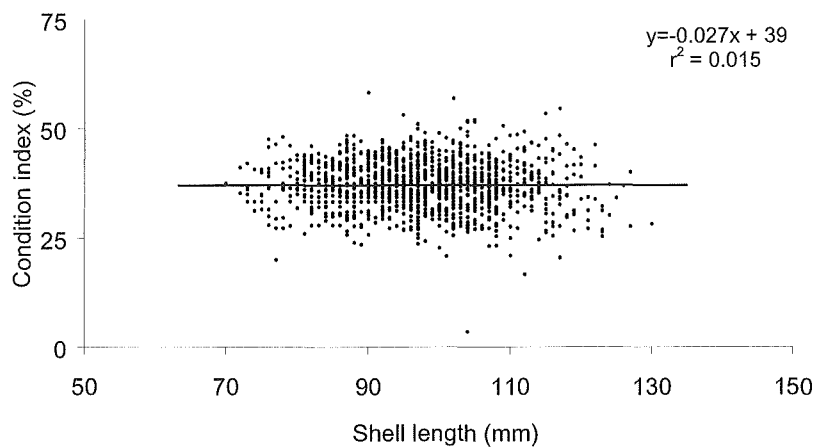


Figure 2. Relationship between cooked weight condition index (%) and shell length (mm) of mussels collected in Pelorus Sound between November 1997 and October 1998 (n=19,088).

APPENDIX 3

Influence of dropper on mussel condition and shell growth

An analysis of condition and shell growth data revealed no significant dropper effect (i.e. stock × site (area) × dropper) ($p > 0.25$). This was expected, as dropper was a level of replication within the model. Therefore condition and shell growth data from replicate droppers were pooled.

APPENDIX 4

Linear shell growth: Chapter 3.

The trajectory of the shell growth of mussels sampled during the experiment in Chapter 3 was linear ($r^2= 0.989$) (Figure 2).

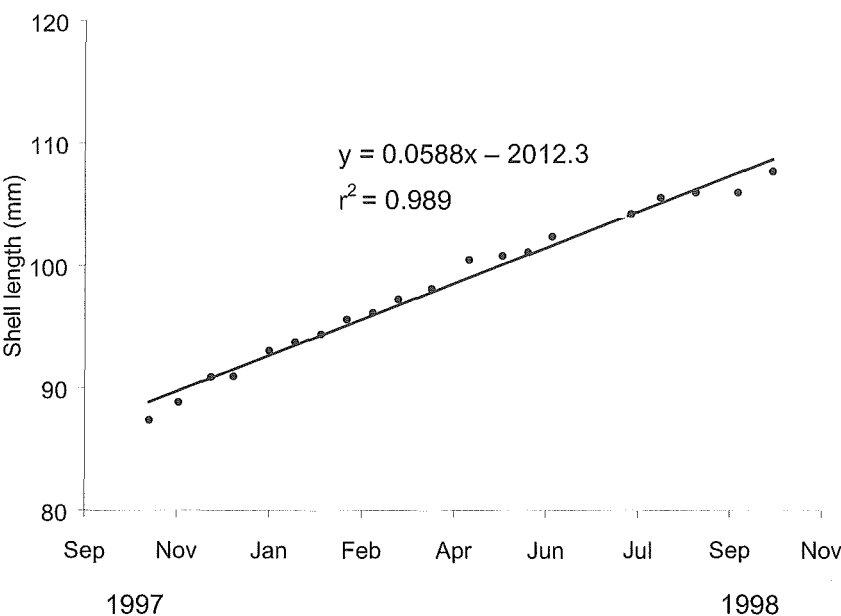


Figure 3. Mean shell length of mussels (all stocks) sampled between November 1997 and October 1998.

APPENDIX 5

Calculation of monthly shell growth rates

Formula 3.1.

$$\text{Monthly shell growth rate} = \frac{\left(\text{Length of each mussel from a defined stock and site at time } t \right) - \left(\text{Mean length of mussels from the same stock and site at time } t-1 \right)}{\text{Time interval between } t \text{ and } t-1 \text{ in months}}$$

APPENDIX 6

Mussel densities: Chapter 3

The density of mussels on the experimental droppers was calculated at the end of the experiment, in Chapter 3, to determine whether density could

explain any of the differences in growth between stocks. No significant differences ($P>0.05$) occurred between stocks (Tables 1 & 2).

Table 1. ANOVA testing whether the density of mussels varied between stocks. Density was the dependent factor and stock was independent.

Factor	d.f Effect	MS Effect	F	p-value
Stock	3	186.2	2.78	0.07
Residual	20	66.9		
Total	23			

Table 2. Mean density of mussel stocks.

Stock	Mean density of mussels per metre of dropper
Golden Bay (small)	84.3
Kaitaia (small)	74.5
Marlborough Sounds (large)	75.8
Kaitaia (large)	85.2

APPENDIX 7

Linear shell growth: Chapter 4.

The trajectory of the shell growth of mussels in each of the three growth trials in Chapter 4 was linear (Figure 3).

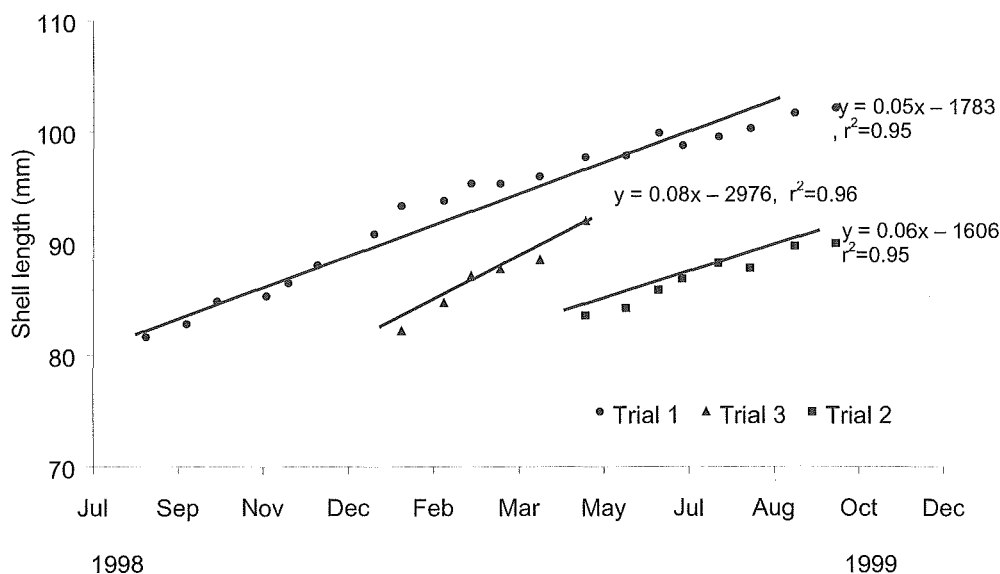


Figure 4. Shell growth of mussels caught in Trial 1, 2, and 3. Shell lengths are the mean for all the stocks in each trial. The equations for the linear trendlines and the r-squared values are given on the graph.

APPENDIX 8

Differences in shell length between stocks within growth trials: Chapter 4.

Significant differences ($p < 0.05$) in shell length occurred between mussel stocks at the start of the three growth trials. For example, the Golden Bay stock was 83 mm and Kaitaia stock was 77 mm, in August 1998, when sampling began in the first growth trial. These differences in length were unexpected as the three stocks were similar sizes (< 3.5 mm) when they were first seeded onto ropes. It appears that small differences in spat sizes between stocks were responsible for the differences in shell length when the growth trials began. Spat seeded onto the ropes in Hallam Cove could have been between 800 and 3200 μ m in shell length (see Methods 4.2.1, Chapter 4). Using data on temporal changes in the length frequencies of cohorts of newly settled *P. canaliculus* (Hayden 1995), it is

possible to estimate that there could have been up to a seven-week difference in age between 800 and 3200 μm long mussels. Because the growth curve of mussels between settlement and death is sigmoidal (Bayne 1976), a seven week difference in age at first seeding could account for the 6 mm difference in shell lengths seen at the start of Trial 1.

Knowledge that relatively small differences in the initial length of spat can result in larger differences at the time of harvest could be useful to farmers. Kaitaia spat is regularly washed ashore in batches consisting of specific size cohorts (Hickman 1976, Pers. Obs.). If mussel farmers have a choice, using batches containing the largest spat would reduce the time it takes for mussels to reach a harvestable size. This observation also has implications for future experiments: if the growth of multiple groups of spat is to be compared, ideally, the groups should be of similar size. In the present study, however, this did prove difficult due to variations in the timing of spat settlement at the three catching sites.

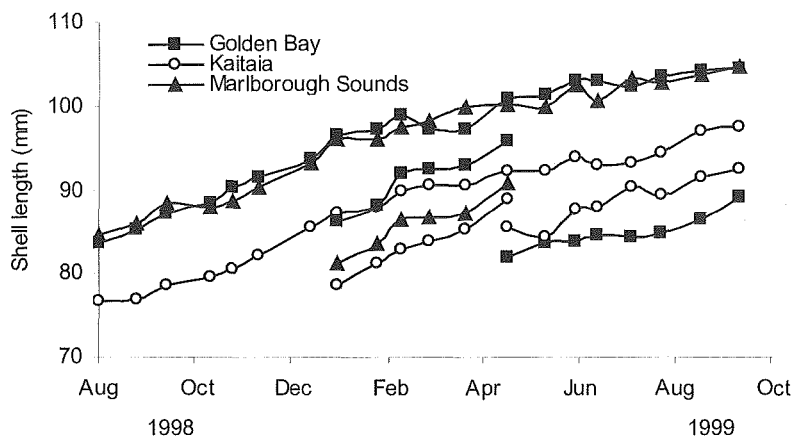


Figure 5. Shell growth of mussel stocks in Trial 1, 2, and 3. Confidence intervals have been omitted from the graph to improve clarity. The mean 95% confidence interval was ± 1.1 and values ranged from 0.8 to 1.8 mm.